

Subnasalveolar Anatomy and Hominoid Phylogeny: Evidence From Comparative Ontogeny

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ABSTRACT The present analysis evaluated extant hominoid subnasal morphological variation from an ontogenetic perspective, documenting both qualitative and allometric details of subnasal maturation in *Hylobates*, great apes and modern humans. With respect to intraspecific variation, results of log-linear modeling procedures indicate that qualitative features of the subnasal region shown previously to discriminate extant taxa (Ward and Kimbel, 1983; McCollum et al., 1993) do not vary appreciably with either age or sex. In terms of quantitative variation, aside from observed changes in the position of the anterior attachment of the nasal septal cartilage relative to the lateral margins of the nasal cavity, the morphology of the subnasal region does not vary appreciably with age. Furthermore, it was found that sexual dimorphism in subnasal form is present only in *Pongo* and *Gorilla* and is the result of sexual bimaturism rather than sexual variation in canine size. In considering interspecific variation in subnasal form, there is a propensity among hominoid taxa for the nasal cavity floor to be free of substantial topographic relief. The smoothly continuous nasal floor topography identified in the majority of hominoid taxa appears to be produced by extensive resorption of the anterior nasal cavity floor that accompanies an upward rotation of the anterior maxilla during craniofacial ontogeny. Comparisons of ontogenetic allometric trajectories indicate that relatively little of the variation in hominoid subnasal form can easily be attributed to variation in body/cranial size. Instead, variation in craniofacial orientation, vascular anatomy and incisor size and inclination were identified as potential mediators of hominoid subnasalveolar anatomy. Although results of this analysis confirm that many details of the orangutan subnasal morphology are derived for this taxon, there is little conclusive evidence to support recent reports that the morphology displayed by *Gorilla* is primitive for great apes (Begun, 1992, 1994). Am. J. Phys. Anthropol. 102:377-405, 1997. © 1997 Wiley-Liss, Inc.

Reconstruction of the phylogenetic history of the Hominoidea has always been complicated by the nature of the fossil sample. With the possible exception of the Samburu Hills maxilla, whose resemblance to modern gorillas has been noted by several workers (e.g., Ishida et al., 1984; Pilbeam, 1986; Andrews and Martin, 1987; Hill and Ward,

1988), a complete absence of any fossils attributable to extant African apes is a persistent problem and what record there is of many fossil hominoid taxa is unfortu-

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nately limited to a small number of isolated teeth and fragmentary cranial and postcranial remains. Given the nature of the evidence, the anatomy of the subnasalveolar region, often well-preserved and well-represented in the fossil record, has emerged as a valuable tool in the analysis of hominoid phylogeny (e.g., Ward and Pilbeam, 1983; Ward and Kimbel, 1983; Andrews and Martin, 1987; de Bonis et al., 1990; Andrews, 1992; Begun, 1992, 1994, 1995; Dean and Delson, 1992; de Bonis and Koufos, 1993).

That the anatomy of the subnasal region may offer evidence bearing upon the phylogenetic relationships among hominoid taxa was originally suggested by Robinson (1953, 1954) following the discovery and analysis of the SK 80 "Telanthropus" maxilla from Swartkrans, Member 1. Some 30 years later, the recovery of a number of maxillofacial specimens attributable to the Miocene genus *Sivapithecus* (Pilbeam et al., 1980; Pilbeam, 1982; Andrews and Tsekaya, 1980) provided the stimulus to assess subnasal morphological variation in extant and fossil apes (Ward and Kimbel, 1983; Ward and Pilbeam, 1983). Analysis of the *Sivapithecus* material resulted in the identification and characterization of morphological patterns that discriminate extant hominoid taxa. The distinctive nature of these morphological patterns has subsequently been confirmed quantitatively (McCollum et al., 1993).

Although most workers are in general agreement regarding the morphological features that distinguish extant taxa, a consensus has yet to be reached concerning the phylogenetic significance of variation observed in subnasal form. Take, for example, the issue of character polarity. In their analysis of extant and fossil forms, Ward and Kimbel (1983) identified the chimpanzee subnasal morphological pattern as being closest to the primitive condition among large-bodied taxa. Shea (1985a, 1988), citing presumed associations between craniofacial orientation (i.e., airorhynch and klinorhynch) and subnasalveolar anatomy, suggested that the morphology displayed by the airorhynch orangutan may be a better representation of the primitive great ape condition. Most recently, Begun (1992, 1994, 1995)

has argued that the gorilla morphology is primitive due to its resemblance to that of both hylobatids and the fossil great ape taxon *Dryopithecus*.

Much of the difficulty in establishing not only the polarity of subnasalveolar variation, but also the more general subject of character homology, derives from our limited understanding of the factors responsible for the differentiation of hominoid subnasal form. For example, it is presently unclear how variation in either body size (both intra- and interspecific) or masticatory adaptation impacts upon subnasalveolar anatomy. As a means of improving our knowledge of this taxonomically important area, the present study examines the ontogeny and comparative anatomy of the extant hominoid subnasal region. The explicit goal of this research is to identify and characterize the developmental and functional parameters that mediate subnasal morphogenesis in hominoid taxa. The results of this research will then be used to assess the phylogenetic significance of variation observed in hominoid subnasal form.

MATERIALS AND METHODS

Sample

Taxonomic samples represent ontogenetic series of *Pongo pygmaeus* (n = 71), *Gorilla gorilla* (n = 93), *Pan troglodytes* (n = 68), *Homo sapiens* (n = 72) and a comparable series of hylobatid crania (n = 69), representing a variety of species.¹ The African ape and human samples are housed in the Hamann-Todd Osteological Collection, Laboratory of Physical Anthropology, Cleveland Museum of Natural History. The *Pongo* and hylobatid samples are derived from the primate collections of the Department of Mammalogy, National Museum of Natural History, Smithsonian Institution. For purposes of analysis, the ontogenetic series were sorted into five sex-segregated age classes defined primarily by molar eruption stage (Table 1). Age classes

¹The hylobatid sample includes representatives of *Hylobates agilis*, *H. concolor*, *H. klossi*, *H. lar*, *H. moloch*, *H. muelleri* and *H. pileatus* as identified from museum records. All taxa differ primarily in body size except for *H. concolor* which displays a distinctive facial profile (Groves, 1972; Marshall and Sugardjito, 1986). Care was taken to include representatives of all taxa in the older age classes so as not to unduly bias characterization of the adult phenotype towards a particular size range.

TABLE 1. Summary of hominoid sample

Dental/cranial developmental stage	<i>Hylobates</i>		<i>Pongo</i>		<i>Gorilla</i>		<i>Pan</i>		<i>Homo</i>	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
1. Deciduous—M ¹ erupting	6	1	6	8	10	9	4	7	7	7
2. M ² erupting	5	5	3	5	16	11	7	6	3	7
3. M ³ erupting	4	5	6	5	2	7	2	4	13	6
4. Patent suture ¹ /canine erupting ²	5	8	12	6	9	9	7	9	4	5
5. Fused suture ¹ /canine erupted ²	18	12	10	10	11	9	11	11	10	11

¹ *Pongo*, *Gorilla*, *Pan*, and *Homo*.² *Hylobates*.

TABLE 2. Qualitative variables

Nasal floor topography	Stepped—Any change in relief at the hard palate/nasal sill transition lateral to the incisive fossa.
Premaxillary/ maxillary suture	Smooth—No change in relief at the hard palate/nasal sill transition. Patent—Any portion of the suture along the nasal cavity floor patent. Fused—Nasal floor aspect completely fused.
Septal groove	Midsagittal trough or groove along nasal sill that represents the continuation of the vomeral (and prevomer) groove along the nasal sill (absent/present).
Incisive crest (<i>Hylobates</i> only)	Midsagittal crest in incisive region derived from the prevomer (absent/present).
Incisive canal partitioning	Incisive canal partitioned by components of osseous nasal septum (absent/present/complete).

TABLE 3. Quantitative variables

Nasoalveolar clivus length	Nasospinale (anterior septal attachment)-prosthion chord.
Nasal sill length ¹	Horizontal chord between lateral margins of the nasal aperture and the posterior pole of the premaxilla.
Septal attachment length ¹	Horizontal chord between anterior septal attachment and the posterior pole of the premaxilla.
Septal attachment position	Septal attachment length divided by nasal sill length.
Degree of separation/overlap ¹	Horizontal chord length between anteriormost aspect of palatine process of maxilla and the posterior pole of the premaxilla.
Palatal thickness	Thickness of the palate immediately posterior to the incisive fossa.
Nasal aperture breadth	Maximum breadth of nasal aperture.
Incisive fossa breadth	Breadth of incisive fossa posterior to posterior pole of premaxilla.
Basiscranial length	Nasion—basion chord.

¹ Measured parallel to the occlusal plane.

beyond the eruption of the third molar are defined by basilar suture (spheno-occipital synchondrosis) patency in great apes and humans (patent/fused) and canine eruption stage in *Hylobates* (erupting/erupted).

Subnasal variables

Variables of interest include both qualitative (Table 2) and quantitative (Table 3; Fig. 1) features of the subnasal region shown previously to discriminate extant taxa (McCollum et al., 1993). The majority of the craniometric data were obtained through direct measurement of the dry skull and were recorded to the nearest 0.1 mm using dial slide calipers or, where necessary (i.e., palatal thickness), to the nearest 0.5 mm using spreading calipers. The degree of separation/overlap of subnasal elements (premax-

illa and maxillary palatine process) was measured in the majority of specimens from lateral radiographs. Prior to radiography, wires were passed into the incisive canal and tightly wrapped around each element. The premaxilla and hard palate were traced from the radiographs and the degree of separation/overlap was measured normal to the occlusal plane.² Separation of subnasal elements was initially scored as a negative value, whereas overlap of elements was recorded as a positive value. For a number of

²The measure of separation/overlap is meant to estimate the length of the palatine fenestra or incisive canal. Measurement of this dimension normal to the occlusal plane rather than normal to the premaxilla was found necessary due to the morphology of the gorilla subnasal region. In this taxon, the differential height of the premaxilla and hard palate within the subnasal region would result in a greatly inflated overlap dimension when measured normal to the premaxilla. Using the occlusal plane as a reference plane of measurement alleviates this problem.

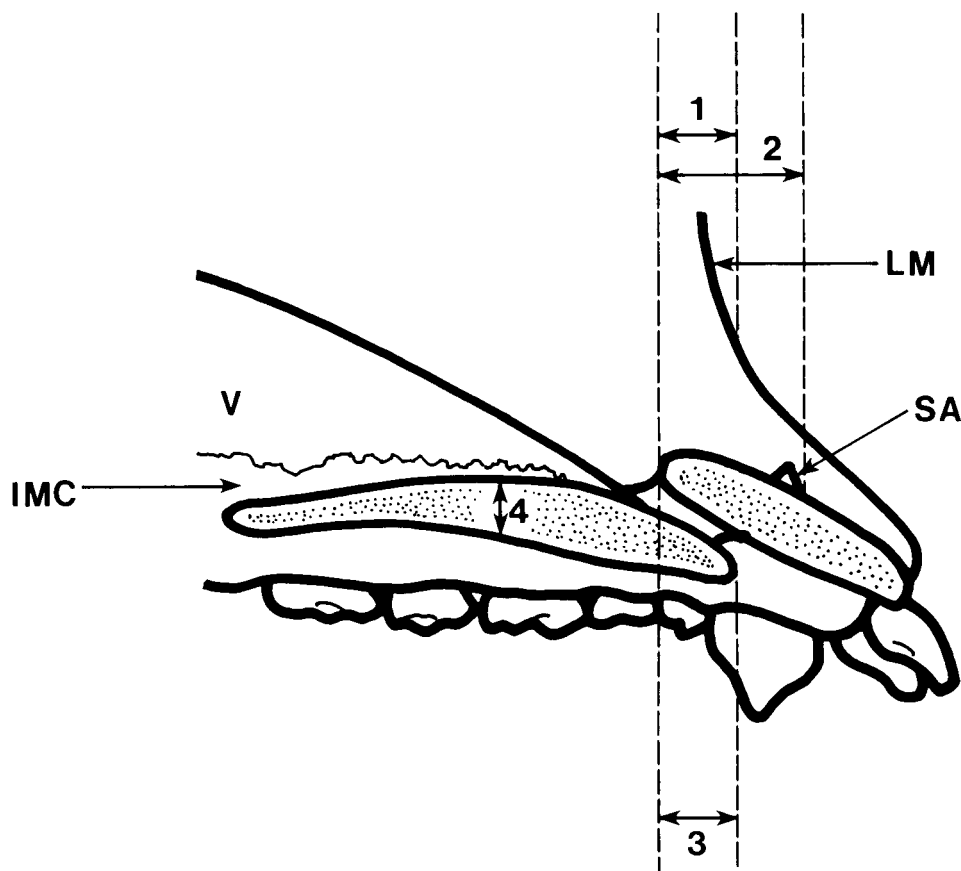


Fig. 1. Schematic sagittal section of the subnasal morphology of an adult chimpanzee illustrating measurements of the subnasal region used in this and previous studies. 1, nasal sill length; 2, septal attachment length; 3, degree of overlap; 4, palatal thickness. See Table 3 for further description. LM, lateral margins of nasal aperture. SA, attachment site for cartilaginous nasal septum; V, vomer; IMC, intermaxillary crest.

the human crania used in this study, sagittal sectioning has damaged the incisive canal, thus preventing reliable wrapping of the subnasal elements. In these specimens separation or overlap of subnasal elements was measured by tracing the hard palate and alveolar process from full-scale photographs of the sagittally-sectioned crania.

Statistical methods

Intraspecific analyses. Log-linear modeling procedures ($P < 0.05$) were used to assess the independence of qualitative subnasal features with respect to both sex and dental/cranial developmental stage. With regard to the quantitative features, reduced major axis (RMA) regression was used to characterize the allometric growth of each

variable relative to basicranial length. It is assumed in these analyses that increase in the latter variable adequately reflects increasing body/cranial size during ontogeny. In these analyses, RMA regression was performed on the means of the natural log-transformed variables calculated for each of the ten single-sex age classes (Table 1). For the degree of separation/overlap, in which negative values were originally recorded, 10 mm was added to each raw value (all taxa) prior to logarithmic transformation.

RMA parameters were calculated separately for each sex and significance of differences in sex-specific slope was determined through calculation of the T-statistic described by Clarke (1980). In cases where

sex-specific slopes were found to be nonsignificant, significance of sex-specific intercepts was evaluated using the "quick test" of Tsutakawa and Hewett³ (1977). Sex-specific variation in the growth and form of the subnasal region was further assessed using analysis of variance (ANOVA, $P < 0.05$). ANOVA was applied to the raw data (individual cases) and used to test for differences in the size of subnasal variables between males and females of common dental developmental stage. In the ANOVA analyses, significance of differences in sex-specific means was assessed using the GT2 method of analysis.

In addition to the analyses described above, which consider the ontogeny of subnasal variables individually, the logged means of all quantitative variables were included within a principal components analysis in order to identify intraspecific *patterns* of subnasal ontogeny. In this multivariate generalization of allometry, the eigenvector, or directional-cosines, of the first principal component extracted from the covariance matrix of logarithmic values, reflects relative proportion changes during ontogeny (Jolicoeur, 1963). In the intraspecific application, a relatively high loading on the allometry vector (i.e., first principal component) indicates that a particular variable increases at a faster relative rate than those variables with lower values. Using this statistical procedure, taxon-specific multivariate patterns of growth are characterized by the sequential ordering of variables along the allometry axis.

Interspecific analyses. Interspecific variation in the growth allometries of individual quantitative subnasal variables was assessed through a series of pairwise analyses. As in the intraspecific analyses, differences in RMA slope or y -intercept calculated for each taxon (combined-sex age class means) were identified using the T-statistic and "quick test," respectively. These analyses considered only those variables which were found to scale significantly with basicranial length during ontogeny and significance of differences in either slope or y -intercept was

assessed at an experimentwise error rate of $\alpha = 0.05$ (Dunn-Sidak adjustment).

RESULTS

Qualitative observations

Spatial and topographic relations of subnasal components. In hylobatids, the maxillary palatine process and premaxilla are completely separated in the sagittal plane by the palatine fenestra which establishes a broad communication between the oral and nasal cavities (Fig. 2). The nasal sill, i.e., that portion of the premaxilla that contributes to the floor of the nasal cavity, is not uniformly flat, but tends instead to be depressed midsagittally, at the attachment for the cartilaginous septum, below the superior apices of the laterally deflected central incisor roots. On either side of the septal attachment, the nasal sill rises superolaterally, over the incisor and canine roots, to become continuous with the rounded lateral margins of the nasal aperture. The lateral aspects of the nasal sill are thus elevated above the hard palate such that gibbons consistently display a "stepped" nasal cavity floor (Table 4).

At this point it is necessary to clarify what specifically is meant by a "stepped" versus a "smooth" nasal floor topography. The topography of the nasal cavity floor refers to the amount of vertical relief that is present at the transition between the nasal sill and the maxillary palatine process along the nasal cavity floor ("stepped" = some vertical relief; "smooth" = absolutely no vertical relief). In this and previous quantitative analyses of hominoid subnasal anatomy (i.e., McCollum et al., 1993) nasal floor topography was scored immediately lateral to the palatine fenestra or incisive fossa/canal for the obvious reason that there will always be a drop, be it either minor or quite substantial, into the palatine fenestra or incisive fossa/canal from the nasal sill. However, in previous discussions (e.g., Ward and Kimbel, 1983; McCollum et al., 1993), the topography of the nasal cavity floor has virtually always been discussed concurrently with incisive fossa/canal size. This has had the unfortunate effect of implying that nasal floor topography is scored more medially, in the immediate vicinity of the incisive fossa. In order to avoid further confusion regarding

³The "quick test" does not test y -intercepts directly. Rather, after fitting a best-fit line through the combined set of data points, the "quick test" uses Fisher's exact test to determine whether the number of points above the curve from one population is random.

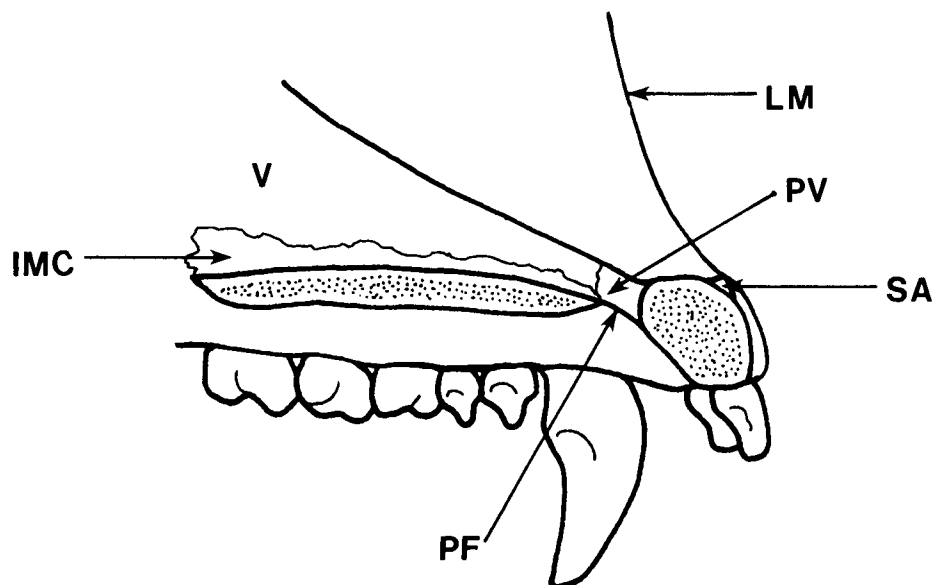


Fig. 2. Schematic sagittal section of the subnasal morphology of *Hylobates*. PV, prevomer; PF, palatine fenestra. See Figure 1 for additional abbreviations.

TABLE 4. *Hylobates* qualitative data¹

Age class	n	Entrance ²	Suture ³	Groove ²	Incisive crest ²
		Stepped/smooth (%)	Patent/fused (%)	Absent/present (%)	Absent/present (%)
1. ♂	6	100/—	83/17	67/—	—/83
1. ♀	1	100/—	100/—	100/—	—/100
2. ♂	5	80/—	80/20	100/—	—/100
2. ♀	5	100/—	80/20	100/—	—/100
3. ♂	4	100/—	100/—	75/25	50/50
3. ♀	5	100/—	60/40	100/—	40/60
4. ♂	5	100/—	20/80	80/20	—/100
4. ♀	8	100/—	12/88	100/—	—/100
5. ♂	18	89/6	6/94	94/6	6/94
5. ♀	12	100/—	8/92	92/—	—/100

¹ Postmortem damage has prevented the accurate scoring of qualitative traits in a number of specimens. For this reason, percentages do not always add to 100.

² Results of log-linear modeling procedures indicate that the distribution of character states for this variable show no significant association with either sex or age.

³ Results of log-linear modeling procedures indicate that the distribution of character states of this variable is not independent of age.

this matter, nasal floor topography and incisive fossa/canal dimensions will be discussed separately in this and future analyses.

In comparison to the condition observed in hylobatids, the premaxilla of great ape taxa normally overlaps the maxillary palatine process at the nasal cavity entrance to form an incisive canal. In *Pongo*, the amount of overlap is substantial and a long, narrow incisive canal is present (Fig. 3a). Lateral to the incisive canal, the transition between the premaxilla and palate along the nasal cavity floor of adults (Age Classes 4 and 5) is

typically free of any topographic relief. However, although a "smooth" nasal floor topography is characteristic of the adult form, a somewhat more "stepped" topography, implying the presence of a slight change in relief between the premaxilla and hard palate, occurs with a greater frequency (but not significantly so) prior to the completed eruption of the anterior dentition (Age Class <3; Table 5).

Contrary to previous reports (e.g., Ward and Pilbeam, 1983; Ward and Kimbel, 1983; McCollum et al., 1993), the African apes cannot reasonably be described as display-

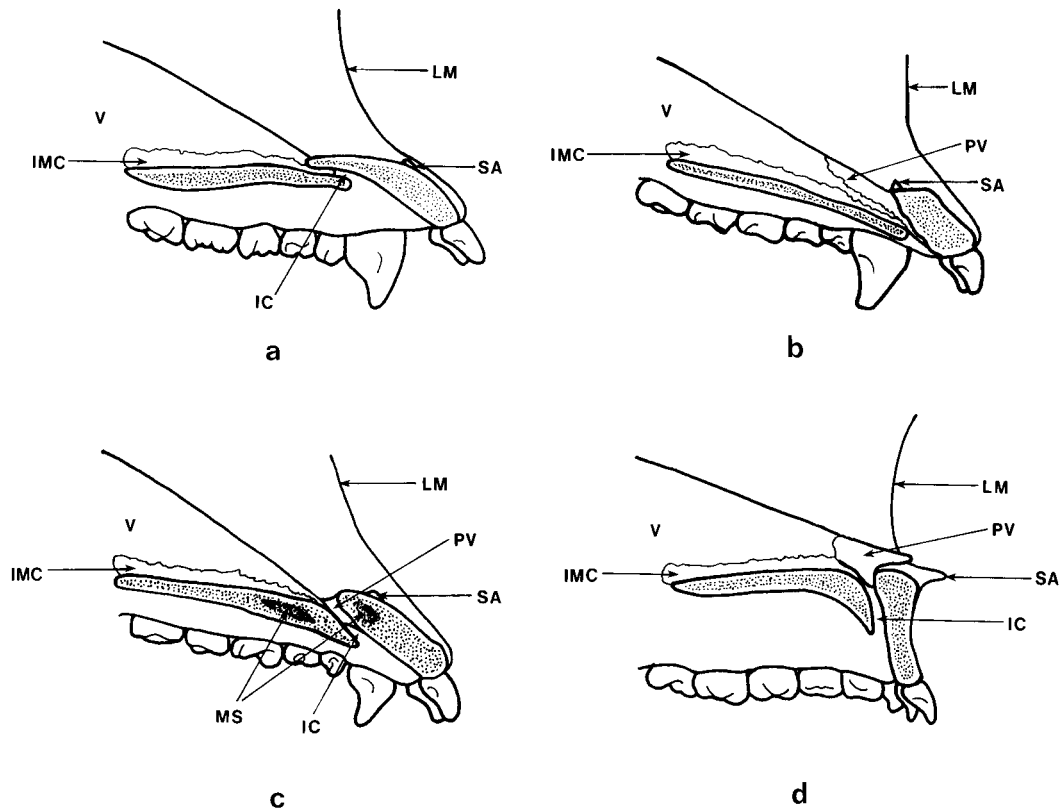


Fig. 3. Schematic midsagittal section of the subnasal region of extant large-bodied hominoids. (a) *Pongo* (IC, inclusive canal); (b) *Gorilla*; (c) *Pan* (MS, maxillary sinus); (d) *Homo*. See Figures 1 and 2 for additional abbreviations.

TABLE 5. *Pongo* qualitative data¹

Age class	n	Entrance ²	Suture ²	Groove ²	Partitioning ²
		Stepped/smooth (%)	Patent/fused (%)	Absent/present (%)	Absent/present (%) (complete)
1. ♂	6	67/33	67/33	—/100	100/—
1. ♀	8	38/63	88/12	—/88	75/13 (—)
2. ♂	3	—/100	100/—	—/100	67/33 (100)
2. ♀	5	40/60	60/40	—/100	100/—
3. ♂	6	17/83	50/33	—/100	100/—
3. ♀	5	—/100	60/40	—/100	60/40 (100)
4. ♂	12	—/100	58/42	25/75	92/8 (—)
4. ♀	6	—/100	50/50	—/100	100/—
5. ♂	10	10/90	30/70	—/100	90/10 (100)
5. ♀	10	—/100	60/40	—/100	100/—

¹ Postmortem damage has prevented the accurate scoring of qualitative traits in a number of specimens. For this reason, percentages do not always add to 100.

² Results of log-linear modeling procedures indicate that the distribution of character states for this variable show no significant association with either sex or age.

ing similar subnasal anatomies. Although both taxa are characterized by a premaxilla that overlaps the hard palate to form an incisive canal, the degree of overlap differs substantially among these taxa (Begun, 1992, 1994, 1995; McCollum et al., 1993). In

Gorilla, the degree of overlap of subnasal elements is considerably less than that observed in *Pongo* and the incisive canal is correspondingly short (Fig. 3b). In comparison, *Pan* is characterized by an amount of overlap of subnasal elements and an incisive

TABLE 6. *Gorilla* qualitative data¹

Age class	n	Entrance ²	Suture ²	Groove ²	Partitioning ²
		Stepped/smooth (%)	Patent/fused (%)	Absent/present (%)	Absent/present (%) (complete)
1. ♂	10	100/—	100/—	30/70	—/100 (20)
♀	9	100/—	78/—	56/33	33/44 (50)
2. ♂	16	94/6	100/—	81/13	13/87 (36)
♀	11	100/—	91/—	82/18	18/73 (25)
3. ♂	2	100/—	100/—	50/50	—/100 (—)
♀	7	100/—	100/—	86/14	14/86 (17)
4. ♂	9	100/—	100/—	100/—	—/100 (56)
♀	9	100/—	100/—	100/—	11/89 (25)
5. ♂	11	100/—	100/—	91/9	—/100 (55)
♀	9	100/—	100/—	100/—	11/89 (50)

¹ Postmortem damage has prevented the accurate scoring of qualitative traits in a number of specimens. For this reason, percentages do not always add to 100.

² Results of log-linear modeling procedures indicate that the distribution of character states for this variable show no significant association with either sex or age.

TABLE 7. *Pan* qualitative data¹

Age class	n	Entrance ²	Suture ²	Groove ²	Partitioning ²
		Stepped/smooth (%)	Patent/fused (%)	Absent/present (%)	Absent/present (%) (complete)
1. ♂	4	50/50	100/—	—/75	75/25 (—)
♀	7	71/29	86/14	14/86	71/29 (—)
2. ♂	7	57/43	29/71	—/100	86/14 (—)
♀	6	17/83	33/67	17/67	50/33 (—)
3. ♂	2	50/50	—/100	—/100	50/50 (—)
♀	4	50/50	25/75	25/75	75/—
4. ♂	7	43/57	—/100	29/71	43/57 (25)
♀	9	67/33	—/75	11/67	67/11 (100)
5. ♂	11	64/36	—/100	64/36	45/55 (17)
♀	11	64/36	—/91	55/36	73/18 (—)

¹ Postmortem damage has prevented the accurate scoring of qualitative traits in a number of specimens. For this reason, percentages do not always add to 100.

² Results of log-linear modeling procedures indicate that the distribution of character states for this variable show no significant association with either sex or age.

canal length that are comparable to those present in the orangutan (Fig. 3c). It should be noted, however, that the diameter of the chimpanzee incisive canal is nevertheless greater than that typical of *Pongo*.

The African apes also differ in terms of nasal floor topography. In *Gorilla*, a substantial change in relief occurs throughout the extent of the nasal sill/hard palate transition. This “stepped” nasal floor topography is characteristic of individuals of all dental/cranial developmental stages (Table 6). Although *Pan* also tends to display “stepped” nasal cavity floors (Table 7), the change in relief present at the hard palate/nasal sill transition is subtle and never approximates the more abrupt condition typical of *Gorilla*. Furthermore, approximately one-third of all adult chimpanzee individuals were scored as displaying a “smooth” nasal floor comparable to that observed in the orangutan. The relative proportion of individuals displaying either a “stepped”

or “smooth” nasal floor is fairly consistent throughout chimpanzee ontogeny (Table 7).

Although modern humans are characterized by an overlap of subnasal elements within the subnasalveolar region, the amount of this overlap is quite small. In sagittal view it is apparent that the long incisive canal characteristic of *Homo* is more a function of the anterior hard palate being flexed against a vertically oriented “premaxilla”⁴ than it is of overlap of subnasal elements along the nasal cavity floor (Fig. 3d). The modern human morphology is associated with an incisive canal diameter that is

⁴The presence of a distinct premaxillary skeletal element in human crania has long been an issue of debate among comparative anatomists and craniofacial biologists (Ashley-Montagu, 1935). Recent study of nasomaxillary ossification in the developing human embryo have revealed that the human “premaxilla” is generated from the intermaxillary secondary ossification centers of the maxilla (i.e., Jacobson, 1955; Wood et al., 1969; Sperber, 1989). The human intermaxilla is homologous to the premaxilla of other mammals in that it encloses the maxillary incisor teeth and forms the alveolar ridge and primary palate (Sperber, 1989).

TABLE 8. *Homo* qualitative data¹

Age class	n	Entrance ²	Suture ³	Groove ²	Partitioning ²
		Stepped/smooth (%)	Patent/fused (%)	Absent/present (%)	Absent/present (%) (complete)
1. ♂	7	43/57	71/29	14/14	100/—
♀	7	43/57	100/—	17/14	100/—
2. ♂	3	—/67	100/—	100/—	100/—
♀	7	57/43	86/14	71/14	71/14 (100)
3. ♂	13	23/77	85/15	54/23	77/23 (—)
♀	6	50/50	83/—	83/—	100/—
4. ♂	4	25/75	50/50	75/—	50/25 (—)
♀	5	20/80	20/80	60/40	80/20 (—)
5. ♂	10	10/90	20/70	40/10	50/50 (20)
♀	10	10/90	10/90	50/10	90/10 (—)

¹ Postmortem damage has prevented the accurate scoring of qualitative traits in a number of specimens. For this reason, percentages do not always add to 100.

² Results of log-linear modeling procedures indicate that the distribution of character states for this variable show no significant association with either sex or age.

³ Results of log-linear modeling procedures indicate that the distribution of character states for this variable is not independent of age.

only marginally greater than that typical of *Pongo*. Although “stepped” nasal floors are more frequently observed prior to the completed eruption of the anterior dentition (Age Class <3), the transition between the nasal sill and palate along the nasal cavity floor is typically free of any relief, much as is observed in *Pongo* (Table 8). In modern humans, it is not uncommon for an elevated ridge, representing the confluence of a well-developed lateral nasal crest with an anteriorly located spinal crest, to be present at the most anterior aspect of the nasal sill (Gower, 1923; McCollum et al., 1993).

Anatomy of the nasal septum. The vomer in *Hylobates* extends anteriorly, along the nasal palatal lamina, only to the palatine fenestra (Fig. 2). Immediately anterior to the vomer, the bony nasal septum is completed by the “perpendicular plate” of the premaxilla, or *prevomer*, a skeletal element generated from a pair of intramembranous ossification centers that become fused to the posterior pole of the premaxilla either pre- or postnatally (De Beer, 1985). The hylobatid prevomer commonly extends anterior-inferiorly along the oral surface of the premaxilla to form a small sagittally oriented crest in the incisive region. Incisive crests, present in individuals of all age classes (Table 4), are notably absent in the smallest hylobatid species, *H. klossi*. The superior margin of the prevomer, like the vomer, includes a septal groove that houses the inferior margin of the nasal septal cartilage. This groove continues anteriorly, along the

nasal sill for some distance. In hylobatids, the attachment site for the cartilaginous component of the nasal septum on the nasal sill extends well anterior to the coronal plane of the nasal aperture’s lateral margins and is occasionally in the form of an anteriorly-projecting spinous process (anterior nasal spine) comparable to that characteristic of modern humans (Fig. 2).

In *Pongo* the vomer usually extends anteriorly along the nasal palatal lamina only to the posterior aspect of the incisive canal. To reach this point, the vomer passes between the premaxillae within a deep septal groove (Fig. 3a). The septal groove of the premaxilla extends anteriorly from the posterior pole for some length and occasionally continues anterior to the nasal aperture’s lateral margins. In some cases the vomer does not reach the posterior pole of the premaxilla and instead terminates just posterior to the incisive canal/fossa. When this occurs the cartilaginous septum continues anteriorly from the vomer to the premaxilla either directly upon the palatal nasal lamina (within a palatal septal groove) or, alternatively, along a small prevomer. In *Pongo*, osseous components of the nasal septum only rarely extend into the incisive canal (Table 5; Schwartz, 1983).

As noted above, the *Gorilla* subnasal morphology is characterized by a marked change in elevation between the palatal nasal lamina and nasal sill (Fig. 3b). In this taxon, the vomer typically extends anteriorly along the palatal lamina to enter the most posterior aspect of the incisive canal. The *Gorilla*

vomer does not, however, contact the premaxilla above. Rather, in these specimens vertical and horizontal continuity between the vomeral septal groove and septal attachment of the nasal sill above is established by a large prevomer. Together, the prevomer and the vomer continue anteroinferiorly, below the premaxilla, to partition the posterior aspect of the incisive canal (Table 6). Complete partitioning of the incisive canal into two tubular channels occurs when a median crest originating from the inferior surface of the premaxilla fuses with the intermaxillary crest of the palate. In *Gorilla*, only young individuals (Age Class <3) are characterized by an extensive septal groove along the nasal sill. During ontogeny, this groove becomes increasingly more limited to the most posterior aspect of the nasal sill.

The anatomy of the chimpanzee nasal septum is similar to that of the gorilla in that a prevomer is a usual component of the osseous portion of the nasal septum (Fig. 3c). However, the prevomer of *Pan* is considerably smaller than that typical of the gorilla. In *Pan*, prevomer and vomeral skeletal elements continue anteroinferiorly into the incisive canal, but complete partitioning of this passageway is restricted to the older age classes and is somewhat more common in males than females (Table 7). In chimpanzees, a groove for the septal cartilage on the nasal sill is present in individuals of all dental/cranial developmental stages and typically extends anteriorly only to the vicinity of the coronal plane defined by the nasal aperture's lateral margins (Table 7).

Like the African apes and hylobatids, the osseous nasal septum of humans is regularly comprised of both vomeral and prevomer elements. Unlike the other apes, however, the modern human vomer extends anteriorly to abut against a prevomer that, in addition to extending inferiorly, underneath the "premaxilla" and only slightly into the incisive canal, also gains an attachment along the superior surface of the nasal sill immediately behind the anteriorly projecting cartilaginous septal attachment (anterior nasal spine; Fig. 3d). As in *Pongo*, the incisive canal is only rarely partitioned by

osseous components of the nasal septum (Table 8; Schwartz, 1983).

Sutural morphology. The premaxillary/maxillary (PM/M) suture of gibbons remains patent throughout much of ontogeny and fuses during the eruption of the permanent canine (Age Class ≥ 4 ; Table 4). In dentally mature individuals (Age Class 5), both the facial and nasal aspects of this suture are normally completely fused, but patency of the prevomer/vomer (PV/V) suture is fairly common. In *Pongo*, fusion of the facial aspect of the PM/M suture begins following the completed eruption of the deciduous dentition (Age Class 1) and is usually complete in full adults (Krogman, 1930; Ashley-Montagu, 1935; Schultz, 1941). Fusion of the nasal aspect of this suture may occur at any time during ontogeny (Table 5). Time of fusion of the PV/V suture (when present) is equally variable.

The full extent (both facial and nasal aspects) of the premaxillary/maxillary, as well as the prevomer/vomer sutures of the *Gorilla* cranium remain patent well into adulthood (Table 6; Ward and Kimbel, 1983). In chimpanzees, fusion of the facial aspect of the PM/M suture begins prenatally and is generally completed prior to the completed eruption of the permanent dentition (Krogman, 1930; Ashley-Montagu, 1935). Complete fusion of the nasal aspect of this suture occurs during eruption of the second permanent molar (Age Class 3). None of the dentally mature individuals within the present sample display patency of this suture within the nasal cavity (Table 7). Time of fusion of the prevomer/vomer suture in *Pan* is also quite variable.

Within the nasal cavity of modern humans, a suture homologous to the premaxillary/maxillary suture of apes can be observed along the lateral walls of the nasal aperture and along the floor of the nasal cavity. The lateral portions of this suture may be patent in infants and children up to the age of five years, but it is far more typical for this aspect of the suture to be totally obscured at birth (Ashley-Montagu, 1935). That portion of the suture along the nasal cavity floor can be observed throughout much of postnatal ontogeny with fusion being sig-

nificantly more common only following eruption of the third molar (Age Class >3; Table 8; Behrents and Harris, 1991). Complete fusion of the maxillary/prevomer suture occurs with the eruption of the second molar (Age Class 2); the prevomer/vomer suture remains patent well into adulthood.

Quantitative data

Intraspecific analyses. As summarized in Table 9, there is a fairly strong correlation between increase (or decrease) in subnasal dimensions and increasing basicranial length in the great ape and hylobatid samples ($|0.80| \leq r \leq |0.99|$). Only the thickness of the palate fails to correlate as strongly with basicranial length in these taxa. In hylobatids, the thickness of the palate is moderately negatively correlated with basicranial length ($r = -0.77$). In *Pan*, these variables are moderately positively correlated ($r = 0.68$). Palatal thickness does not correlate with basicranial length in either *Pongo* or *Gorilla*. Additional variables uncorrelated with basicranial length in the nonhuman samples include both the relative position of the anterior septal attachment and the degree of separation of subnasal elements in hylobatids and the length of the septal attachment in *Gorilla* and *Pan*. In modern humans, only the length of the nasoalveolar clivus and relative position of the septal attachment are strongly correlated with basicranial length ($r = 0.91$ and -0.81 , respectively). The remaining modern human subnasal variables demonstrate either a relatively weak correlation with basicranial length (nasal sill, septal attachment, nasal aperture breadth) or no correlation at all (degree of overlap, palatal thickness, incisive fossa breadth).

In the nonhuman samples, allometric coefficients derived from RMA line-fitting techniques indicate either isometric or moderate positive allometric growth of the majority of subnasal dimensions relative to that of the basicranium (Table 9). Notable exceptions to this finding include the length of the nasoalveolar clivus which increases considerably faster than basicranial length in all species except the gorilla which is otherwise characterized by a relatively slowed rate of clivus growth. Very strong positive allometry also

TABLE 9. Reduced major axis regression statistics

Vs. basicranial length	r^1	y intercept	Slope	95% CL of slope ²
Aperture				
<i>Hylobates</i>	.93	-2.76	1.29	1.06-1.92
<i>Pongo</i>	.90	-5.59	1.91	1.35-2.70
<i>Gorilla</i>	.88	-5.95	1.91	1.31-2.79
<i>Pan</i>	.91	-3.52	1.44	1.04-2.01
<i>Homo</i>	.74	-0.49	0.78	0.41-1.18
Incisive fossa				
<i>Hylobates</i>	.97	-6.66	2.00	1.64-2.44
<i>Pongo</i>	.80	-5.46	1.64	1.02-2.62
<i>Gorilla</i>				
(Male)	.99	-4.80	1.50	1.16-1.94
<i>Gorilla</i>				
(Female)	.99	-7.10	2.00	1.55-2.58
<i>Pan</i>	.82	-7.13	2.00	1.27-3.14
<i>Homo</i>	.24 ns	—	—	—
Clivus				
<i>Hylobates</i>	.83	-10.04	2.86	1.84-2.44
<i>Pongo</i>	.99	-7.68	2.45	2.08-2.88
<i>Gorilla</i>	.99	-4.51	1.64	1.27-2.11
<i>Pan</i>	.93	-8.35	2.56	1.90-3.43
<i>Homo</i>	.91	-4.10	1.56	1.00-1.95
Sill				
<i>Hylobates</i>	.93	-1.51	1.00	0.74-1.34
<i>Pongo</i>	.90	-3.13	1.36	0.95-1.96
<i>Gorilla</i>	.89	-3.03	1.27	0.88-1.83
<i>Pan</i>	.92	-4.81	1.67	1.22-2.28
<i>Homo</i>	-.70	0.33	-0.67	-0.34--1.04
Separation/overlap				
<i>Hylobates</i>	.55 ns	—	—	—
<i>Pongo</i>	.78	-5.11	1.82	1.11-2.97
<i>Gorilla</i>	.93	-1.55	0.91	0.68-1.22
<i>Pan</i>	.90	-7.57	2.33	1.65-3.31
<i>Homo</i>	-.07 ns	—	—	—
Septum				
<i>Hylobates</i>	.91	-17.15	4.57	3.28-6.37
<i>Pongo</i>	.83	-4.79	1.64	1.05-2.54
<i>Gorilla</i>	.55 ns	—	—	—
<i>Pan</i>	.55 ns	—	—	—
<i>Homo</i>	.69	-2.08	1.00	0.51-1.58
Position				
<i>Hylobates</i>	-.49 ns	—	—	—
<i>Pongo</i>	-.82	5.77	-1.36	-0.87--2.14
<i>Gorilla</i>	-.83	7.42	-1.45	-0.94--2.26
<i>Pan</i>	-.77	26.76	-6.00	-3.64--9.88
<i>Homo</i>	-.81	-13.06	3.11	1.76-4.44
Palate				
<i>Hylobates</i>	-.77	12.06	-3.00	1.82-4.94
<i>Pongo</i>	.20 ns	—	—	—
<i>Gorilla</i>	.26 ns	—	—	—
<i>Pan</i>	.68	-20.54	4.78	2.71-8.42
<i>Homo</i>	-.20 ns	—	—	—

¹ ns, nonsignificant; all other coefficients significant at $P < 0.05$.

² RMA confidence limits (CL) are asymmetric by definition.

characterizes growth of the septal attachment in hylobatids and palatal thickening in the chimpanzee. In humans, the length of the nasoalveolar clivus scales positively allometric with basicranial length. With the exception of the position of the anterior septal attachment, which rapidly extends outside of the nasal cavity during ontogeny, growth of the remaining human subnasal

TABLE 10. Results of ANOVA¹

	<i>Hylobates</i>	<i>Pongo</i>	<i>Gorilla</i>	<i>Pan</i>	<i>Homo</i>
Aperture	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5
Incisive fossa	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5
Clivus	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5
Nasal sill	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5
Overlap	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5
Septum	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5
Position	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5
Palate	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5
Basicranium	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5

¹ Analysis of variance: Numbers represent age classes. Significant sex-specific means ($P < 0.05$) are indicated in bold italics.

TABLE 11. Eigenvectors of the first principal component listed in ascending order

<i>Hylobates</i>		<i>Pongo</i>		<i>Gorilla</i>		<i>Pan</i>		<i>Homo</i>	
Palate	-0.365	Position	-0.282	Position	-0.304	Position	-0.715	Overlap	-0.170
Position	-0.241	Palate	0.061	Palate	-0.003	Basicranium	0.128	Nasal sill	-0.153
Nasal sill	0.148	Basicranium	0.221	Overlap	0.221	Aperture	0.158	Aperture	-0.007
Basicranium	0.151	Nasal sill	0.286	Basicranium	0.260	Septum	0.173	Inc. fossa	0.021
Aperture	0.208	Inc. fossa	0.293	Nasal sill	0.325	Nasal sill	0.198	Septum	0.044
Overlap	0.289	Septum	0.328	Septum	0.340	Inc. fossa	0.208	Basicranium	0.168
Inc. fossa	0.290	Overlap	0.354	Inc. fossa	0.393	Overlap	0.266	Clivus	0.172
Clivus	0.320	Aperture	0.389	Clivus	0.424	Clivus	0.303	Palate	0.545
Septum	0.671	Clivus	0.561	Aperture	0.486	Palate	0.413	Position	0.768
Eigenvalue proportion of total variance (%)									
73		77		56		70		50	

variables is moderately negatively allometric (i.e., nasal sill length, length of the septal attachment and breadth of the nasal aperture) relative to increasing basicranial length.

Sexual variation in the growth trajectories of individual subnasal variables is not common in extant hominoid taxa. In hylobatids, *Pan* and *Homo*, sex-specific growth trajectories for all subnasal features were found to be ontogenetically scaled (i.e., both b and y -intercepts not significantly different; Table 9). In these taxa, minimal sexual variation in adult cranial/body size results in a general absence of sexually dimorphic subnasal features in adults (Table 10). In the highly sexually dimorphic orangutan, sex-specific growth trajectories of all subnasal variables were also found to be ontogenetically scaled. However, in this taxon, males of Age Classes 4 and 5 (young and full adults, respectively) display significantly greater basicranial and nasoalveolar clivus lengths than females (Table 10). In addition, fully adult male orangutans (Age Class 5) display significantly greater overlap measures than do females of comparable age. In *Gorilla*, all variables except incisive fossa breadth were found to be ontogenetically

scaled among sexes (Table 9). The significantly different slopes identified for gorilla sexes indicate that females broaden their incisive fossae at a faster relative rate than do males. As a result, females possess incisive fossae of comparable absolute size to those of larger males (Table 10). In *Gorilla*, both young and fully adult males (Age Classes 4 and 5) display basicranial length measures that are significantly greater than those of females and ANOVA results also indicate that young adult males (Age Class 4) display significantly longer nasoalveolar and nasal sill lengths than females of comparable age.⁵

Results of the multivariate analyses (Table 11) indicate that, with the exception of *Gorilla* and *Homo* in which the first principal component extracted from the covariance matrix accounts for only 56% and 50% of the total variation, respectively, the allometry axes identified in the remaining multivariate analyses account for approximately 70–80% of the total variation observed within each sample. The patterns of maturation identified through multivariate procedures

⁵The significantly different value of basicranial length observed at Age Class 1 reflects the female growth spurt identified for this taxon (Shea, 1985b).

(Table 11) accord well with those obtained from the bivariate analyses (Table 9). Increase in the length of the nasoalveolar clivus is one of the major dimensional changes that occurs during subnasal maturation in the nonhuman taxa and increase in the length of the septal attachment and thickness of the palate dominate subnasal ontogeny in hylobatids and chimpanzees, respectively. Multivariate results also confirm that nonhuman subnasal maturation is characterized by a gradual retreat of the anterior septal attachment within the nasal capsule. Humans differ most notably from the apes in that the anterior nasal spine becomes increasingly more anteriorly located during ontogeny.

Interspecific analyses. In general, interspecific comparisons reveal considerable variation in the growth allometries characteristic of quantitative subnasal variables (Table 12). Of the variables considered, only the growth allometries identified for the breadth of the nasal aperture and the breadth of the incisive fossa were found to be broadly similar in all nonhuman taxa. The patterns of growth identified for the remaining subnasal dimensions vary considerably among taxa in terms of slope, y -intercept or both. Results of the interspecific comparisons will be considered more fully in the ensuing Discussion.

DISCUSSION

The ontogeny of subnasal form

Intraspecific variation. Results of the present study indicate that aside for a tendency for the nasal aspect of the premaxillary/maxillary suture to fuse during the later stages of craniofacial ontogeny, the morphology of the subnasal region tends not to vary appreciably with age in extant hominoid taxa. This is particularly true of qualitative variables which vary only slightly, if at all, among age groups. Not unexpectedly, with only a few exceptions (e.g., palatal thickness in hylobatids, nasal sill length in humans), subnasal dimensions increase with age. However, only in chimpanzees does the vertical thickness of the hard palate increase substantially during ontogeny (Fig. 4). In this taxon, palatal thickening during

TABLE 12. Results of interspecific comparisons

	<i>Hylobates</i>	<i>Pongo</i>	<i>Gorilla</i>	<i>Pan</i>
Aperture				
<i>Pongo</i>	ns/ns ²			
<i>Gorilla</i>	ns/ns	ns/ns		
<i>Pan</i>	ns/ns	ns/ns	ns/ns	
<i>Homo</i>	*/- ³	*/-	*/-	*/-
Inc. fossa				
<i>Pongo</i>	ns/ns			
<i>Gorilla</i> ¹	ns/ns	ns/ns		
<i>Pan</i>	ns/ns	ns/ns	ns/ns	
<i>Homo</i>	-/-	-/-	-/-	-/-
Sill				
<i>Pongo</i>	ns/ns			
<i>Gorilla</i>	ns/ns	ns/*		
<i>Pan</i>	ns/ns	ns/*	ns/ns	
<i>Homo</i>	*/-	*/-	*/-	*/-
Clivus				
<i>Pongo</i>	ns/ns			
<i>Gorilla</i>	ns/ns	*/-		
<i>Pan</i>	ns/ns	ns/*	ns/*	
<i>Homo</i>	*/-	*/-	ns/ns	*/-
Septum				
<i>Pongo</i>	*/-			
<i>Gorilla</i>	-/-	-/-		
<i>Pan</i>	-/-	-/-	-/-	
<i>Homo</i>	*/-	ns/ns	-/-	-/-
Position				
<i>Pongo</i>	-/-			
<i>Gorilla</i>	-/-	ns/*		
<i>Pan</i>	-/-	*/-	*/-	
<i>Homo</i>	-/-	*/-	*/-	*/-
Overlap				
<i>Pongo</i>	-/-			
<i>Gorilla</i>	-/-	*/-		
<i>Pan</i>	-/-	ns/ns	*/-	
<i>Homo</i>	-/-	-/-	-/-	-/-
Palate				
<i>Pongo</i>	-/-			
<i>Gorilla</i>	-/-	-/-		
<i>Pan</i>	*/-	-/-	-/-	
<i>Homo</i>	-/-	-/-	-/-	-/-

¹ Combined sex sample.

² ns, nonsignificant.

* Significant at experimentwise error rate of $\alpha = 0.05$; - = not evaluated statistically.

ontogeny is associated with the formation of a *recessus palatinus*, a medial extension of the maxillary air sinus within the structure of the hard palate (Fig. 5; Cave and Haines, 1940; Tobias, 1967; Ward and Kimbel, 1983; Brown and Ward, 1988; Koppe and Schumacher, 1992). Invasive pneumatization of the chimpanzee palate occurs as the functionally independent palatal laminae (nasal and oral) become increasingly more separated from one another during growth (Moss and Young, 1960).

Aside from dimensional changes, the only other notable variation in subnasal form observed between infant and adult crania concerns the relative position of the anterior-

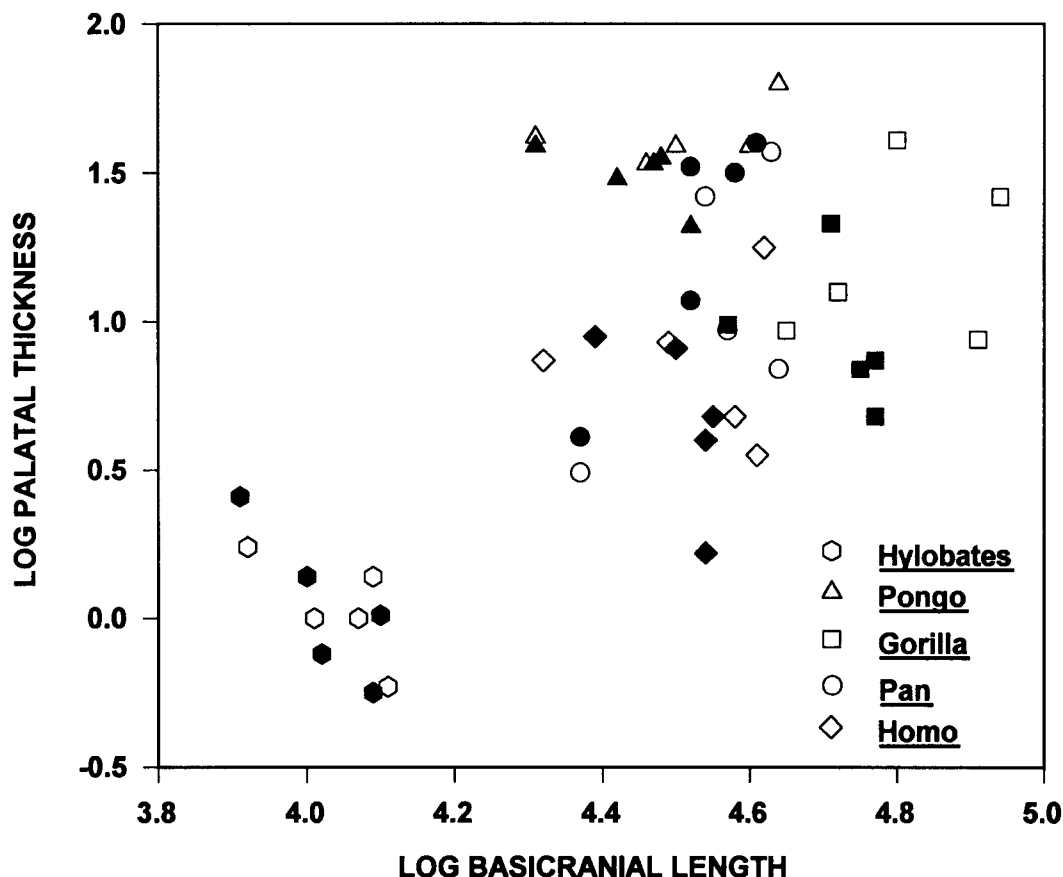


Fig. 4. A plot of palatal thickness versus basicranial length in extant hominoids (hollow, males; filled, females).

most aspect of the cartilaginous septal attachment within the nasal cavity. In the nonhuman taxa, the position of this feature relative to the lateral margins of the nasal aperture is more posterior in adults than in infants. In *Hylobates*, *Pongo* and *Pan*, the anterior septal attachment initially occurs well outside the nasal capsule (Fig. 6), but over time this feature gradually retreats to assume its adult position either slightly anterior to (hylobatids) or approximately within (*Pongo* and *Pan*) the plane of the lateral margins of the nasal aperture. In gorillas, the septal attachment of infants already occurs in the vicinity of the aperture's lateral margins (Fig. 6). With increasing age this feature comes to lie behind the nasal aperture's lateral margins; deep within the nasal capsule (Clarke, 1977).

In comparison with nonhuman taxa, the anterior septal attachment in modern humans becomes increasingly more anteriorly located with age (Fig. 6). Anterior repositioning of the modern human anterior nasal spine reflects the pattern of facial remodeling that is characteristic of this taxon. In modern humans, the anterior surface of the maxilla, including the full extent of the nasoalveolar clivus save the septal cartilage attachment, is resorptive rather than depository as it is in other primates (Enlow, 1968, 1990; Bromage, 1985, 1989). Resorption of the anterior maxillary surface during modern human ontogeny results not only in an apparent anterior migration of the anterior nasal spine, but also the decreasing length of the nasal sill (Table 9). Beyond these features, the modern human subnasal mor-



Fig. 5. An X-ray of an adult chimpanzee demonstrating the invasive pneumatization of the hard palate. The oral and nasal palatal laminae are indicated by wire.

phological pattern is further distinguished from that typical of other hominoids in terms of palatal form ("flexed" against a vertically transposed "premaxilla"). During the course of this investigation, it was observed that the anterior palate of infant great apes, like that of adult humans, is often vertically flexed against the premaxilla (Fig. 7). In this regard, the "flexed" human palate may represent a paedomorphic feature of modern human crania.

Previous quantitative analyses of subnasal form have failed to identify significant sexual dimorphism within the morphological patterns that characterize extant taxa (Ward and Kimbel, 1983; McCollum et al., 1993) and results of the present analysis confirm that sexual variation in cranial/body size is not generally revealed in subnasal form (Tables 9, 10). This is certainly true with respect to qualitative variables whose relative frequencies do not vary significantly between sexes (Tables 4–8). Of the quantitative variables considered, only those relating to the overall size of the premaxilla (e.g.,

nasoalveolar clivus length, nasal sill length, degree of overlap) tend to differ significantly between sexes of the highly dimorphic *Pongo* and *Gorilla*.⁶ Although potentially a product of sexual variation in canine size, the findings that premaxillary features are ontogenetically scaled among sexes and that sexual dimorphism is expressed only among sexes of young and full adults indicate instead that this variation is a function of the sexual bimaturism, i.e., the extended period of male postnatal growth, that has been previously demonstrated for these taxa (Shea, 1985b; Leutenegger and Masterson, 1989; Masterson and Leutenegger, 1992; see Ravosa, 1991).

Interspecific variation. The primary goal of this ontogenetic study was to identify

⁶That sexual variation in *Gorilla* should be restricted to young adults only, as ANOVA results suggest, has no obvious biological explanation. Once attained, sexual dimorphism is expected to be maintained into the fully adult age class. The failure for ANOVA techniques to identify sexual dimorphism within full adults may be a product of either the nature of the data (cross-sectional rather than longitudinal data) and/or our reliance upon the conservative GT2 method for determining significance of means (Sokal and Rohlf, 1980).

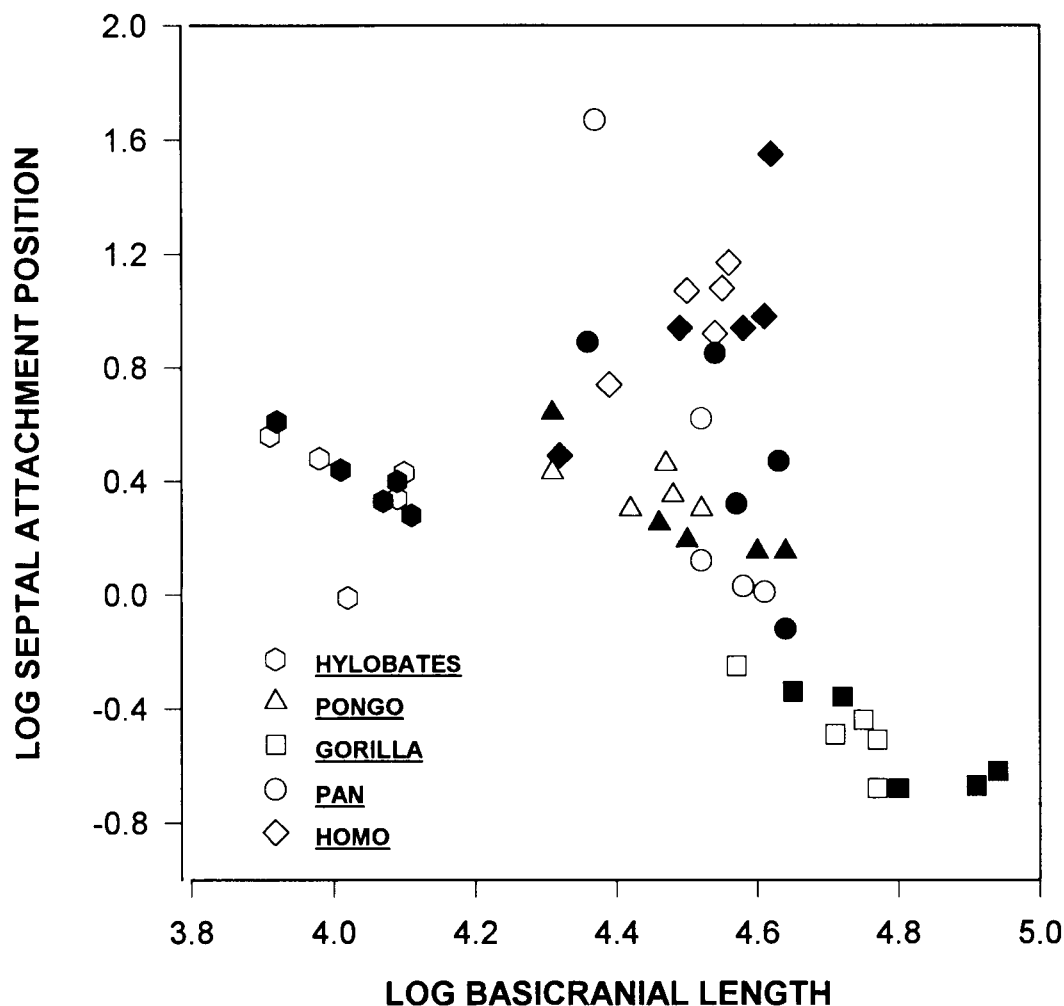


Fig. 6. A plot of septal attachment position versus basicranial length in extant hominoids (hollow, males; filled, females). A value of 0 indicates a septal attachment within the coronal plane of the nasal aperture's lateral margins.

some of the factors responsible for the differentiation of subnasal form in hominoid taxa. However, as a preliminary element of this analysis, it would be helpful to first identify some of the developmental constraints on subnasal form that may be common to all taxa. These constraints, i.e., biases on the production of variant phenotypes or limitations on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system (Maynard Smith et al., 1985), can only be understood with reference to the development of the nasal cavity floor which, for purposes of

this analysis, is considered to include both the palatal nasal lamina, as well as that portion of the premaxilla posterior to the anterior attachment of the cartilaginous septum.

During ontogeny, growth of the respiratory mucosa, nasal conchae and cartilaginous nasal septum results primarily in an increase in the vertical height of the nasal airway and osseous portion of the nasal septum and secondarily in an anteroinferior displacement of the nasomaxillary skeleton (Moss, 1964; Kean and Houghton, 1987; Enlow, 1990; Alberius and Friede, 1992).

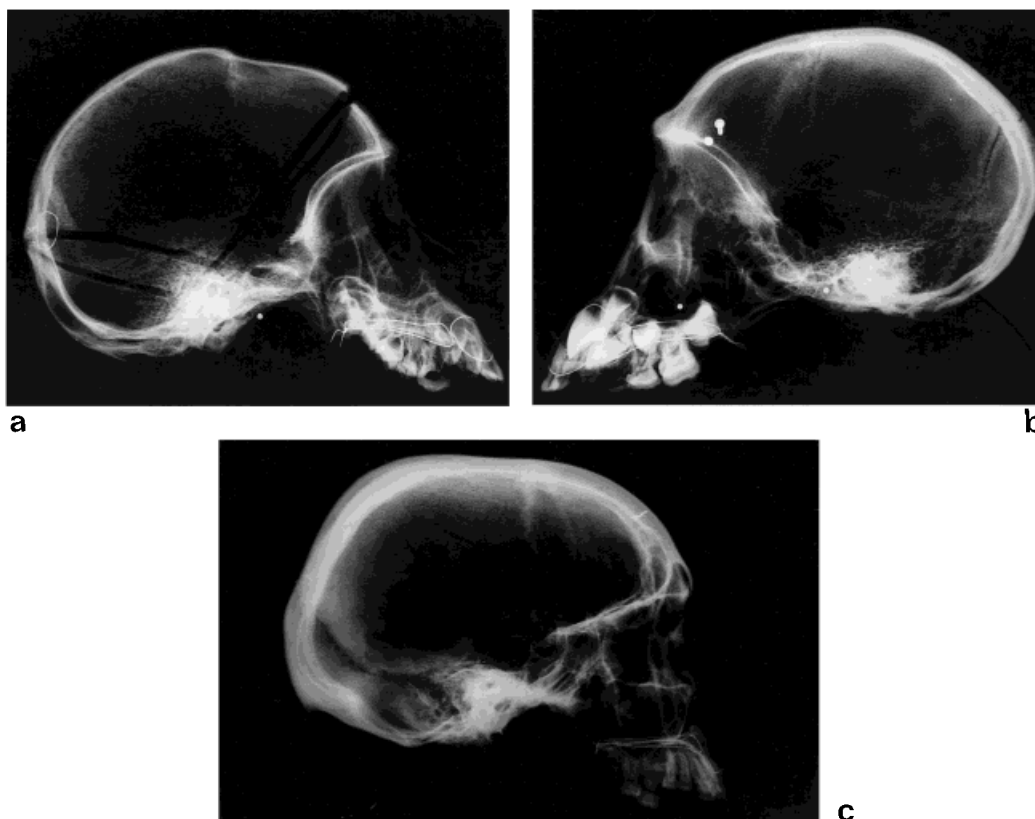


Fig. 7. Lateral radiographs of (a) infant *Gorilla*, (b) infant *Pan*, and (c) adult *Homo*, with the hard palate and premaxilla delineated by wire. Note the flexure of the palate against the premaxilla in the young apes.

The anteroinferior translation of the nasomaxillary complex is normally accompanied by a varying degree of vertical rotation of the anterior maxilla (Björk and Skieller, 1972, 1976). Forward or upward rotation occurs when vertical maxillary growth is greater posteriorly than anteriorly. Backward or downward rotation occurs when vertical growth of the maxilla exceeds that which occurs posteriorly. It has been reported that in extant hominoids vertical growth of the maxilla is greatest posteriorly and these taxa are all characterized by an upward rotation of the maxilla during ontogeny (Enlow and Azuma, 1975; Bromage, 1992).

Upward rotation of the maxilla during ontogeny results in a reorientation of the nasal cavity floor in relation to the otherwise positionally stable nasal functional capsule

(Fig. 8). However, the overall enlargement and normal functioning of the soft tissue that lines this capsule, a pseudostratified columnar ciliated epithelium with goblet cells overlying a highly vascularized and glandular lamina propria (Cormack, 1993), regulate the activity of the osteogenic tissues (i.e., periosteum) and reestablish proper spatial relations (see Enlow, 1990 for further details of bone remodeling). On the nasal surface, the transverse plane of the nasal cavity floor, defined and maintained by the osseous nasal septum through its early stabilization with the anterior cranial base, is restored by increased resorptive activity along the anterior nasal cavity floor (Björk and Skieller, 1976).

The extensive resorption of the anterior nasal cavity floor that occurs during ontog-

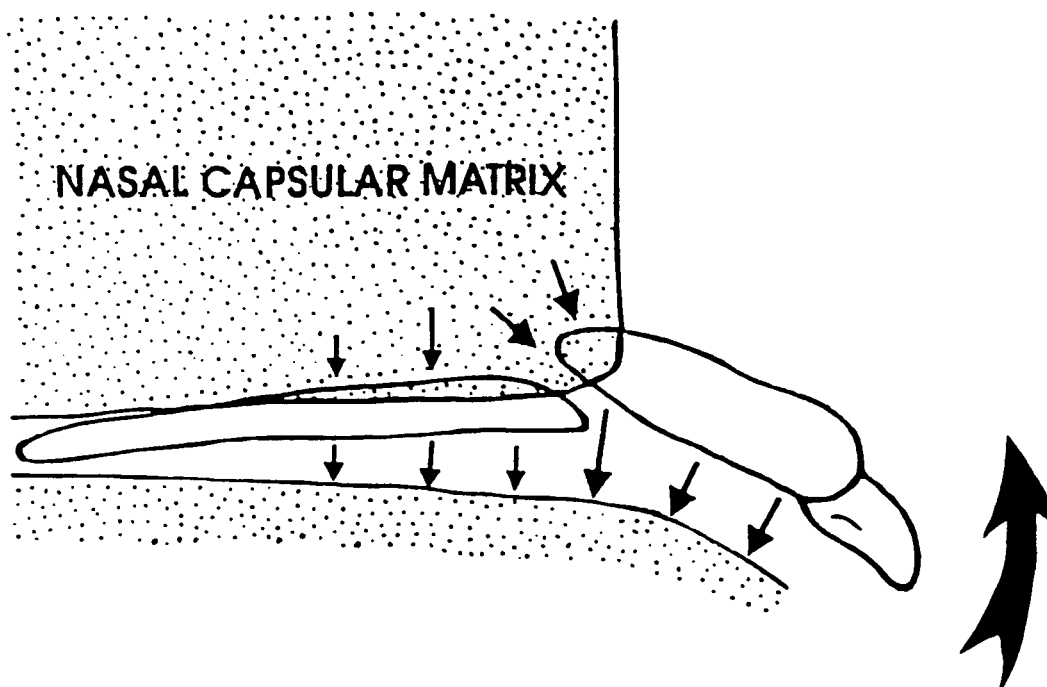


Fig. 8. Remodeling activities accompanying upward maxillary rotation during ontogeny. Upward rotation (large arrow) effects increased resorptive activity (top small arrows) along the anterior nasal cavity floor. Also accompanying this process but not discussed in the text is depositional activity orally (bottom small arrows).

eny should, in hominoids, in which this region most frequently consists of two overlapping elements, result in a nasal cavity entrance that is free of significant topographic relief. Results of the present analysis confirm that there is indeed a propensity for hominoids to display a smoothly continuous transition between the hard palate and premaxilla at the nasal cavity entrance. Although there tends to be some vertical separation between the palatal nasal lamina and premaxilla in *Pan*, the orangutan, chimpanzee and modern human subnasal morphologies all meet the expectation of a general absence of marked vertical relief at the nasal cavity entrance. In the nonhuman taxa, and in particular *Pan*, some vertical separation between the hard palate and premaxilla variably occurs. This topographic relief is most likely the consequence of the exclusive attachment of the osseous septum to the palatal nasal lamina and the septal cartilage to the nasal surface of the premaxilla. This particular morphological configura-

tion allows for some developmental independence of subnasal components along the nasal cavity floor. In modern humans, the extension of the osseous nasal septum onto the superior surface of the "premaxilla" precludes any vertical separation of nasal floor components and thus serves as an additional "constraint" upon the topography of the nasal cavity entrance. It is of note that the "robust" australopithecines also display a remarkably "smooth" nasal floor topography similar to that characteristic of both *Pongo* and modern humans (Robinson, 1954; Clarke, unpublished; Ward and Kimbel, 1983; McCollum et al., 1993). The "smooth" nasal floor of *Paranthropus* is similar to that of modern humans in that it is associated with an osseous septum that extends onto the superior surface of the premaxilla (McCollum, 1977).

The frequent occurrence of smoothly continuous nasal cavity floor topographies among hominoid taxa argues against this feature carrying much phylogenetic weight.

This is particularly true when this feature is considered in isolation from the remainder of the nasal skeleton. For example, the suggestion has been made that the shared possession of "smooth" nasal floors in *Pongo* and modern humans provides evidence of their sister taxa affinities (e.g., Schwartz, 1984). However, a closer look at the subnasal morphologies typical of these taxa reveal that their remarkably smooth nasal floors are each a product of very different developmental influences. In *Homo*, a "smooth" nasal floor occurs by virtue of its characteristic osseous septum morphology. In *Pongo*, a "smooth" nasal floor may relate to the extreme form of airorhynch displayed by this taxon (Shea, 1985a, Brown and Ward, 1988; Ross and Henneberg, 1995; see below).

Given the proclivity of the respiratory mucosa to minimize relief between the palatal nasal lamina and nasal sill in hominoid taxa, the substantial change in relief that occurs at the hard palate/nasal sill transition in both hylobatids (Table 4) and *Gorilla* (Table 6) is in need of explanation. With regard to the *Hylobates* morphology, it should be kept in mind that although the remodeling of the palatal nasal lamina that accompanies maxillary rotation is mediated primarily by the spatial demands of the nasal cavity, the morphology of the premaxillary contribution to the nasal cavity floor must not only conform to the spatial requirements of the nasal cavity, but also to those of the permanent incisors developing within. The morphology of the hylobatid nasal sill, in which the septal attachment tends to be depressed between laterally deflected incisor roots, suggests an overriding influence of the anterior dentition on the morphology of the nasal sill and anterior nasal floor.

The *Gorilla* subnasal morphology is truly unusual among hominoids in that the anterior attachment of the nasal septum occurs well behind the plane of the nasal aperture's lateral margins, at the posterior pole of the premaxilla (Fig. 3b). That portion of the nasal sill posterior to the septal attachment rapidly descends down to the level of the palatal nasal lamina, giving the premaxilla a sharply truncated appearance in sagittal view (Ward and Kimbel, 1983). In the gorilla, the abrupt change in relief between the

premaxilla and palate defines the anterior extent of the respiratory mucosa and nasal tissues. The evidence provided by the hard tissue anatomy therefore suggests that, in comparison to the condition observed in other hominoid taxa, the soft and hard tissue structures of the gorilla nasal capsule are more internalized within the facial skeleton. Consequently, the premaxilla, which makes a substantial contribution to the nasal cavity floor in other taxa including hylobatids, is largely excluded from the remodeling activities of the respiratory mucosa in *Gorilla*. Definitive explanations for the unusual subnasal configuration of gorillas are not immediately apparent, but Shea's (1983) finding that the nasal aperture is more inferiorly positioned in the facial skeleton of gorillas than chimpanzees may be particularly relevant to this issue.

Given the constraints likely to be placed upon the morphology of the hominoid subnasal region by the developmental process, it is possible to consider some of the factors potentially responsible for the differentiation of subnasal form among taxa. Shea (1985a, 1988) suggested that variation in the orientation of the palate relative to the cranial base may underlie some of the variation in subnasal form observed between *Pongo* and the African apes. It was specifically proposed that downward rotation of the face and palate, as would occur with the transition from an airorhynch (*Pongo*) to a more klinorhynch (African apes) skull form, would necessarily result in a relatively greater deflection of the hard palate below the premaxilla. It was argued that this greater deflection of the palate below the premaxilla was responsible for both the "stepped" nasal cavity floor and a relatively broad incisive canal characteristic of African ape taxa.

In the present study, the finding that approximately 30% of all adult chimpanzees possess a "smooth" nasal floor similar to the condition observed in the more airorhynch orangutan, as well as the observation that a relatively wide incisive canal occurs in chimpanzee crania in which the palatal nasal lamina does not deflect substantially below the nasal sill, argue against the simple correlation between craniofacial orientation

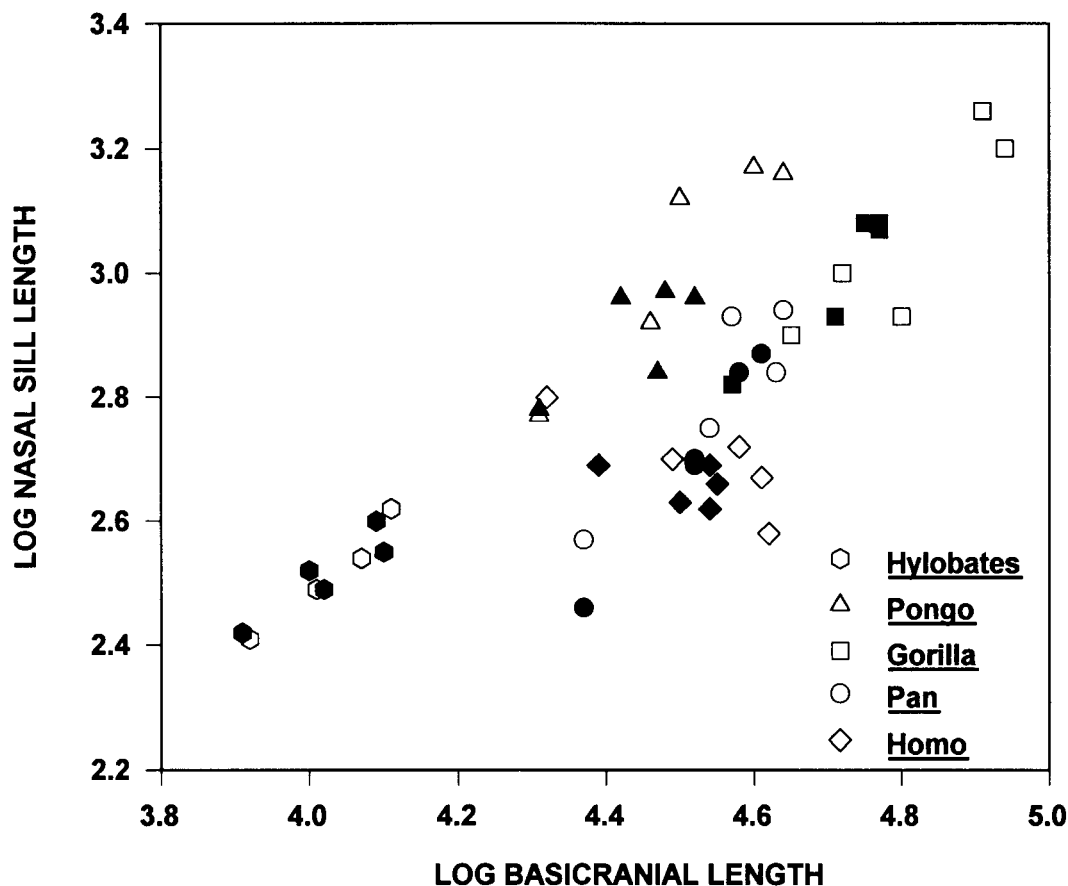


Fig. 9. A plot of nasal sill length versus basicranial length in extant hominoids (hollow, males; filled, females). See text for discussion.

and subnasal form. This does not, however, imply that subnasal morphology is entirely unrelated to craniofacial orientation. Shea's argument was based upon a working assumption that airorhynch, to the degree typical of the extant orangutan, is the primitive condition for hominoid taxa and that the more klinorhynch condition typical of African apes is a derived morphology. More recently it has been found that in comparison to nonhominoid primates, all nonhuman hominoid taxa are characterized by more dorsally deflected palates relative to their basicranial angles, i.e., they are *all* airorhynch (Ross and Henneberg, 1995). However, among hominoids, the degree of facial kyphosis varies considerably. For example, in comparison to the condition displayed by hylobatids, which is perhaps more typical of

the primitive morphotype, orangutans are considerably more airorhynch, whereas that African apes may be somewhat less so (Brown and Ward, 1988; Ross and Henneberg, 1995). It may well be that the extremely smooth nasal floor typical of the orangutan (in comparison to *Pan*), as originally suggested by Shea, as well as the frequent absence of a prevomer identified in the present study both reflect an arrangement of subnasal components that is specifically associated with extreme airorhynch. Interestingly, variation in the relative length of the nasal sill observed among taxa corresponds well with documented variation in facial kyphosis (Table 12; Fig. 9). This finding further suggests the possible relationship between this character and craniofacial orientation. Alternatively, the relatively

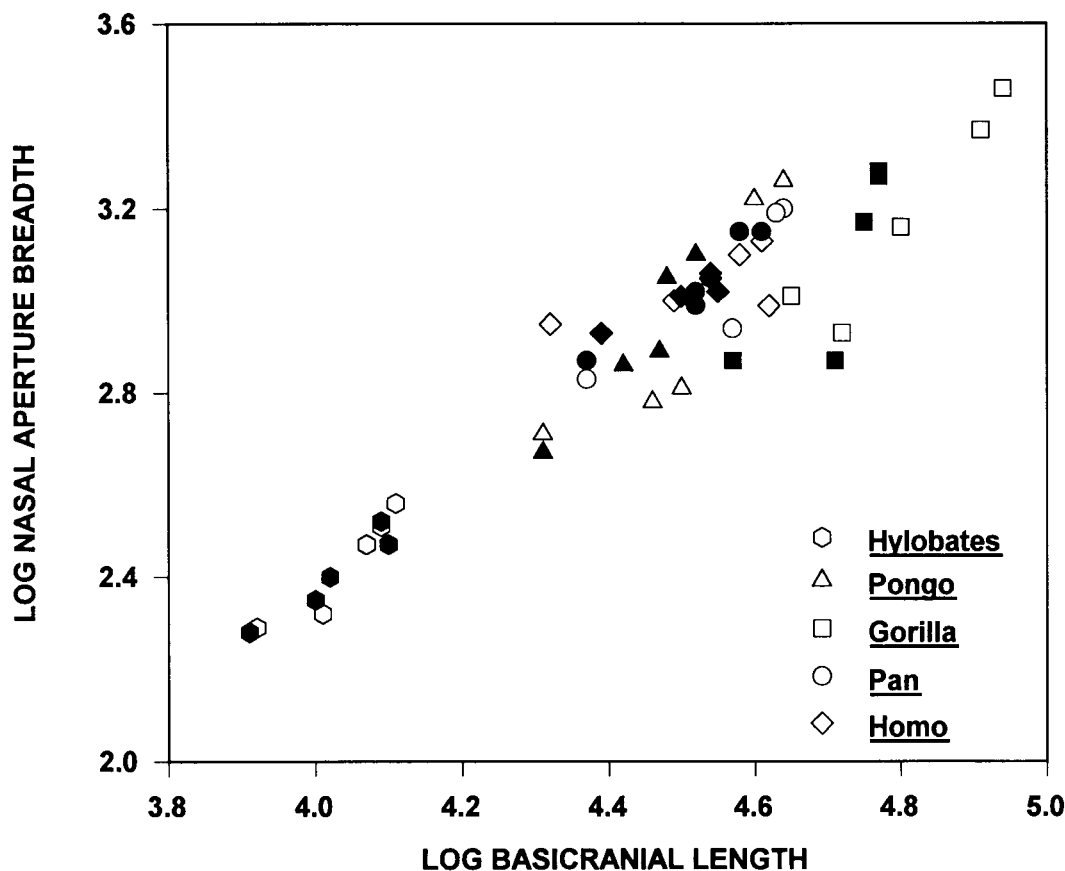


Fig. 10. A plot of nasal aperture breadth versus basicranial length in extant hominoids (hollow, males; filled, females).

short nasal sills of the African apes may relate to their possession of more vertically oriented maxillary incisors (Dean and Delson, 1992). As for variation in the caliber of the incisive canal, it was originally proposed that a reduction in the contents of the neurovascular bundle within the incisive canal could account for the reduced caliber of the incisive canal in *Pongo* (Ward and Kimbel, 1983). This seems a much more plausible explanation for the variation in incisive canal diameter observed among these taxa.

Another factor potentially responsible for some of the interspecific variation observed in subnasal form is body size. Ontogenetic growth allometries, by serving as criteria of subtraction, are often used to distinguish taxonomic variation related to body size from that resulting from nonsize-related

factors (Shea, 1985c). In general, a finding of ontogenetic scaling among taxa suggests that observed variation may be a simple product of the extension of a common trajectory of growth into new size ranges and therefore the result of body size variation. In the present analysis, the finding that the breadth of the nasal aperture breadth is ontogenetically scaled in all nonhuman taxa indicates that much of the interspecific variation in this feature simply reflects body size differences (Table 12). Note that although statistically similar to those of other nonhuman taxa, the allometric growth trajectory identified for the breadth of the nasal aperture in gorillas is nevertheless vertically transposed below those of the remaining nonhuman taxa (Fig. 10). According to Shea (1983), the downward shifts in regression of

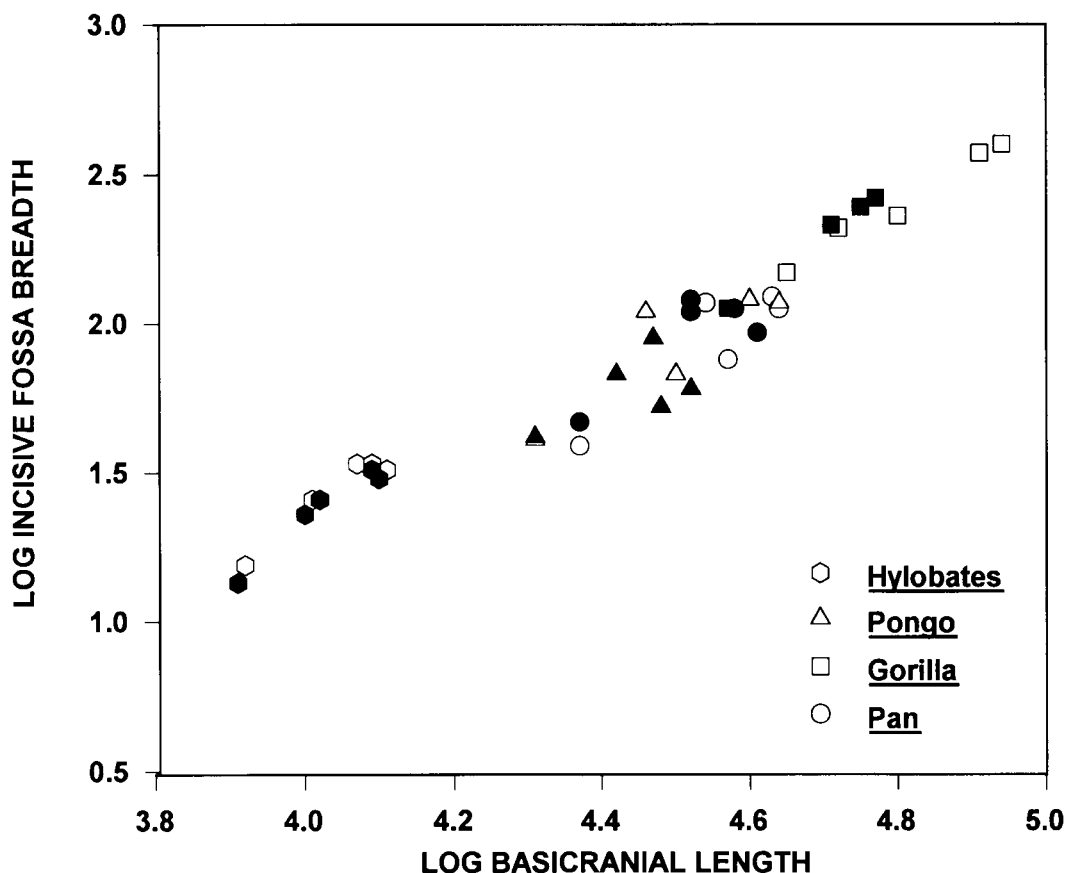


Fig. 11. A plot of incisive fossa breadth versus basicranial length in extant hominoids (hollow, males; filled, females). See text for discussion.

skull widths relative to basicranial lengths commonly observed in the African apes are size-related in that they reflect a reorganization of proportions during growth associated with differences in absolute brain size. In comparison to nonhuman taxa, human infants tend to display a somewhat broader nasal aperture than is expected for hominoids of their cranial size (Fig. 10). However, a relatively slowed rate of aperture growth during human ontogeny (Table 9) results in adults possessing nasal aperture breadths of a dimension comparable to those of apes of similar skull size (Fig. 10). The broader aperture of young humans may reflect the reduced size of the canine. In the apes, the aperture's lateral margins coincide with relatively large canine roots.

That the breadth of the incisive fossa is ontogenetically scaled in all nonhuman taxa also suggests that interspecific variation in this feature, largely reflects differences in cranial/body size (Table 12). However, although statistically similar, the growth trajectory observed for hylobatids is nevertheless vertically transposed above those of the other samples (Fig. 11). Furthermore, it is apparent that infant gorillas display incisive fossa breadths that actually exceed those observed in fully adult orangutans and chimpanzees (Fig. 11). Gorillas thus retain the same allometric relationship between incisive fossa size and basicranial length as is found in the remainder of the great apes, but do so within a broader incisive fossa. Thus, both hylobatids and goril-

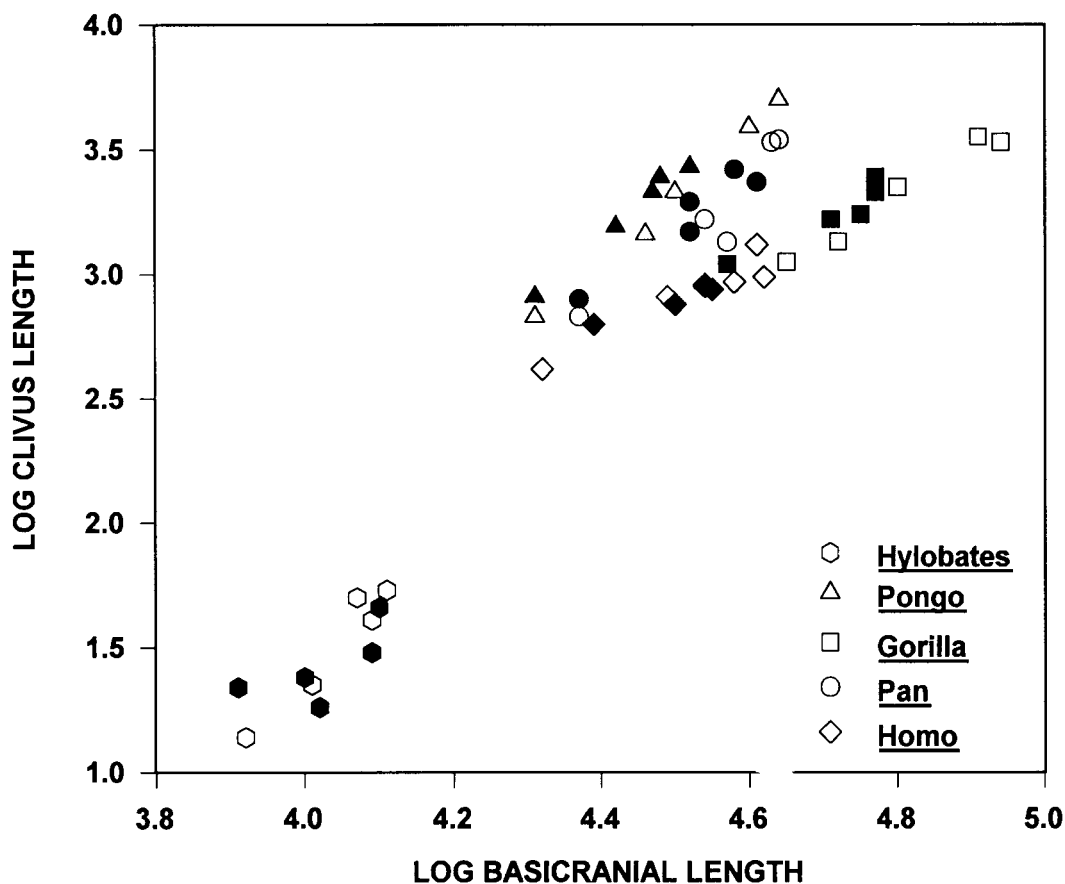


Fig. 12. A plot of clivus length versus basicranial length in extant hominoids (hollow, males; filled, females).

las can be characterized as displaying somewhat broader incisive fossae than other taxa. That these taxa also display substantial relief at the nasal cavity entrance suggests that the breadth of the incisive fossa may be mediated in part by the topography of the nasal sill/hard palate transition. It is of interest that the reduced caliber of the *Pongo* incisive canal is not reflected as a similarly reduced incisive fossa.

Of the remaining subnasal features, only variation in the length of the nasal sill displayed by African apes may prove to be related to variation in cranial/body size (Table 12; Fig. 9). That this is the only feature of the subnasal region that is ontogenetically scaled among these taxa serves to emphasize the truly distinctive nature of the African ape subnasal morphologies.

The remaining interspecific variation in subnasal form shows no clear association with differences in cranial/body size. Rather, the pattern of variation observed for some subnasal features suggests instead their relationship with details of the masticatory apparatus. For example, variation in the length of the nasoalveolar clivus observed among taxa corresponds quite well with variation in incisor dimensions. Among taxa, the length of the nasoalveolar clivus is longest in *Pongo* and *Pan* and considerably shorter in hylobatids, *Gorilla* and *Homo* (Fig. 12). Similarly, the distribution of overlap measures among great ape taxa also tends to correspond with interspecific variation in incisor size (Fig. 13). Given the significance of afforded variation in both the size of the premaxilla and extent of overlap

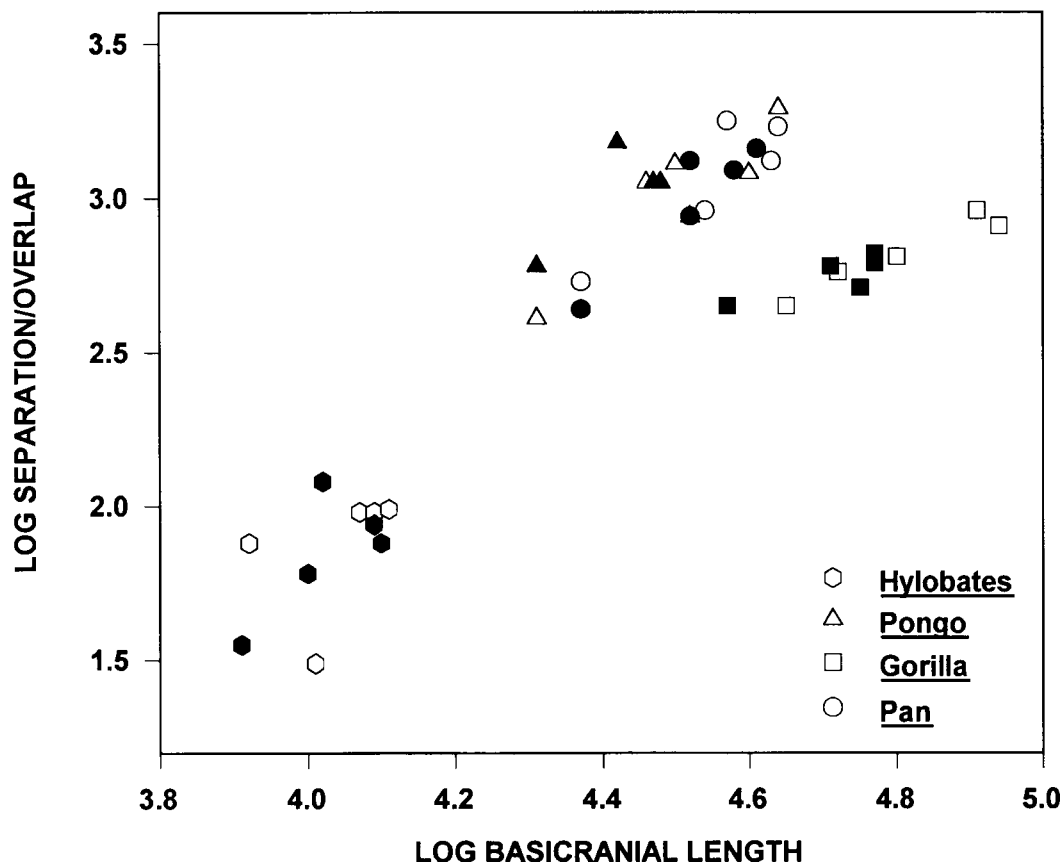


Fig. 13. A plot of separation/overlap of subnasal elements versus basicranial length in extant hominoids (hollow, males; filled, females). Increasing y -values indicate decreasing separation (and increasing overlap) of subnasal elements.

of subnasal elements in recent analyses of hominoid phylogeny (e.g., Begun, 1992, 1994, 1995; Dean and Delson, 1992), further evaluation of the potential influence of incisor size and shape on subnasal form is certainly warranted.

Phylogenetic considerations

In the majority of primate taxa, the maxillary palatine processes and nasal sill are widely separated from one another within the nasal cavity due to the presence of the palatine fenestra. Our own preliminary, unpublished observations of the subnasal region of cercopithecoids crania housed in the Cleveland Museum of Natural History suggest that in these taxa, only that portion of the premaxilla that serves as the site of the septal attachment occurs in the same trans-

verse plane as the palatal nasal lamina. Lateral to the septal attachment, the nasal sill rises superolaterally to become continuous with the lateral margins of the nasal aperture. As a result of this configuration, the nasal aperture takes on a characteristic diamond-shape appearance and there is an abrupt change in relief (a "step") between the lateral aspects of the nasal sill and the palatal nasal lamina along the nasal cavity floor.

Among hominoid primates, only hylobatids display a subnasal morphology comparable to that typical of cercopithecoids in which a wide palatine fenestra separates the premaxilla from the hard palate along the nasal cavity floor. This feature, along with the "stepped" nasal cavity floor, are both characters of the hylobatid subnasal

morphology retained from the ancestral catarrhine condition and therefore primitive for the Hominoidea. Unfortunately, in the absence of additional details concerning the extent of variation present in cercopithecoid subnasal form, it is presently unclear how the remaining characteristic features of the hylobatid subnasal morphology compare with the primitive catarrhine condition. For example, in the absence of quantitative data concerning details of the cartilaginous septum in Old World monkeys, it is not known whether the long, anteriorly projecting septal attachment of gibbons has been retained from an ancestral morphotype or represents an autapomorphic feature of hylobatids. Similarly, the phylogenetic significance of the relatively short nasoalveolar clivus of gibbons is uncertain, as this dimension may be more a reflection of functional parameters (dietary preference?) than of phylogenetic affinities.

It is evident, however, that in comparison to Old World monkeys, hylobatids and indeed all extant hominoid taxa display a broad, flat nasal cavity floor. The transversely broad inferior nasal aperture characteristic of hominoids must reflect a reorganization of the facial skeleton in these taxa. It may well be that the transition to a more airohynch skull form documented for hominoids by Ross and Henneberg (1995) underlies the variation in nasal sill morphology observed among catarrhine taxa. Alternatively, these same researchers found that extant nonhuman hominoids differ from other taxa in that the former species is characterized by more ventrally deflected orbital axes for their palatal orientation. Perhaps it is this particular morphological transformation, being more specific to the facial skeleton itself, that forms the basis of nasal sill variation among catarrhine groups.

Although an overlap of subnasal elements distinguishes all large-bodied hominoid taxa from the primitive subnasal morphology displayed by hylobatids, it is presently unknown whether an overlap of subnasal elements has been retained from the common ancestor of great apes and humans or was acquired independently in varying degrees in the Asian and African clades. Begun (1992, 1994, 1995) has argued that a moder-

ate degree of overlap of subnasal elements and correspondingly short incisive canal, most similar to the condition observed in *Gorilla*, was in fact present in the common ancestor of the great ape/human clade. This conclusion is based upon his identification of these features in two heavily reconstructed *Dryopithecus* specimens (RUD 12 and RUD 44/47) from Hungary. However, the illustrations of these specimens recently provided by Begun (1994: Fig. 17) do not clearly demonstrate an overlap of subnasal elements as in gorillas, but instead reveal a subnasal configuration not unlike that commonly observed in hylobatids (Fig. 14). Until more definitive data are presented to justify the characterization of the *Dryopithecus* morphology, such as quantitative verification of an overlap of subnasal elements, there is little reason to believe that a moderate amount of overlap of subnasal elements characterized the primitive great ape condition.

In the absence of additional data from fossil specimens, it is difficult to establish with any certainty the evolutionary polarity of the variation in subnasal form observed among great ape taxa. However, a number of conclusions regarding the potential phylogenetic significance of this variation are evident from the results of the present analysis. With respect to the subnasal morphology characteristic of the orangutan, it is clear that this taxon displays a form of airohynch that is extreme among hominoids and considerably different from the presumably primitive condition characteristic of hylobatids (Ross and Henneberg, 1995). In light of this conclusion, any feature of the *Pongo* subnasal region found to relate to this distinctive skull form is derived for *Pongo* as opposed to primitive for Hominoidea and/or great apes. The results of this study suggest that the "smooth" nasal floor, long nasal sill and variable absence of a prevomer are all subnasal features related to extreme airohynch and therefore derived for this taxon. Additional derived features of the *Pongo* subnasal morphology include a reduction in both the vascular contents and overall diameter of the incisive canal. It is of note that extreme airohynch and a reduced-caliber

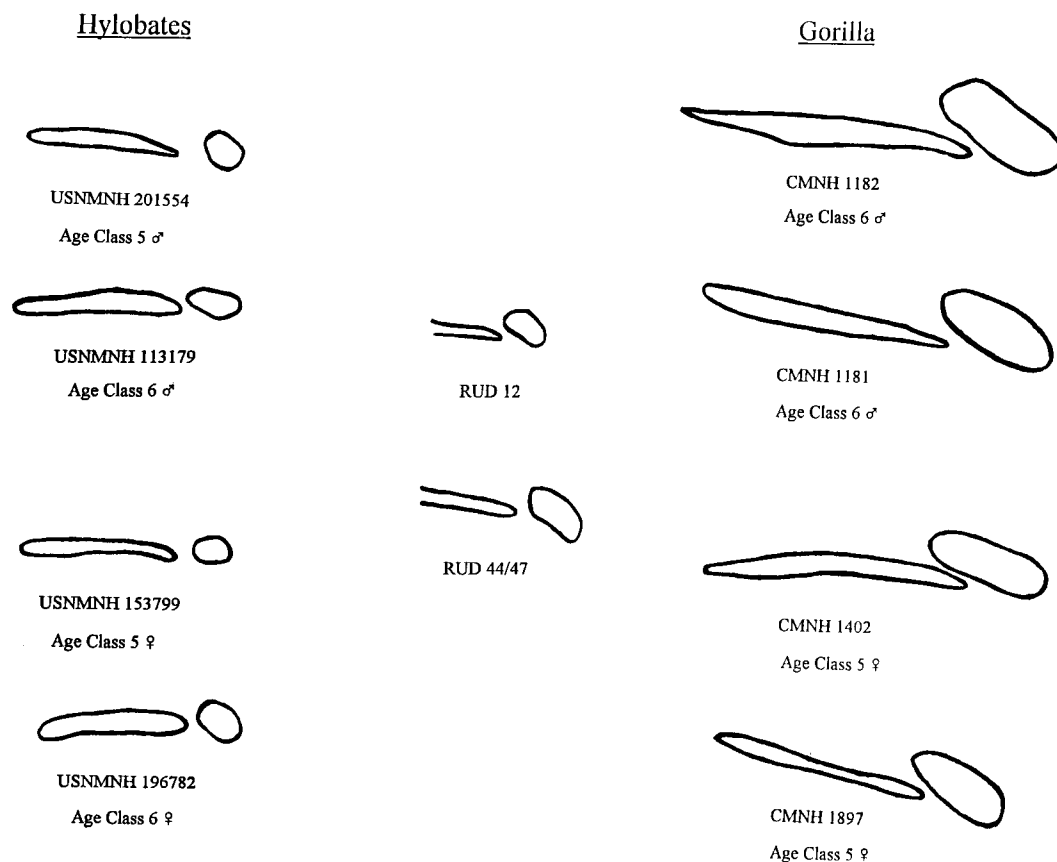


Fig. 14. Tracings of the premaxilla and hard palate of hylobatids and gorillas as obtained from lateral radiographs demonstrating the variation in separation/overlap documented for these taxa.

incisive canal are features also characteristic of *Sivapithecus* (Brown and Ward, 1988). Together, these characters of the craniofacial skeleton remain some of the strongest evidence in support of the existence of a *Pongo/Sivapithecus* clade.

With respect to the African apes, Begun (1992, 1994, 1995) has identified the *Gorilla* subnasal morphology as primitive for great apes because it shares with *Hylobates* a comparatively short premaxilla, a "stepped" nasal floor topography and a relatively large incisive foramen. However, the conclusion that these features, which are presumably also characteristic of *Dryopithecus*, are indeed homologous is not at all certain. For example, the covariation of premaxillary length with incisor dimensions among hominoid taxa is consistent with the conclusion

that a relatively short premaxilla is functionally convergent in these taxa. Of greater significance, however, is the finding that the "stepped" nasal floor (and consequently broad incisive fossae?) of gorillas is only superficially similar to that found in hylobatids. As discussed above, the abrupt change in relief between the premaxilla and palate in the gorilla cranium defines the anterior extent of the nasal cavity floor. In this regard, the "stepped" subnasal morphology of *Gorilla* differs from that of hylobatids where the change in relief between the palatal nasal lamina and nasal sill occurs along the nasal cavity floor (i.e., behind the anterior septal attachment). These findings suggest that the *Gorilla* and hylobatid morphologies, like those characteristic of *Pongo* and *Pan*, are largely convergent.

CONCLUSIONS

The present analysis examined the ontogeny and comparative anatomy of the extant hominoid subnasal region. With regard to intraspecific variation, results indicate that, aside from changes in the relative position of the anterior septal attachment within the nasal capsule, the overall form of the subnasal region does not vary appreciably with age. Significant sexual variation in subnasal form is limited to *Pongo* and *Gorilla*. In these taxa, sexual bimaturism, i.e., a relatively longer duration of male postnatal growth, results most noticeably in males possessing a significantly longer nasolabial clivus than is typical of females.

From a consideration of the development of the nasal cavity floor, it is apparent that there is a propensity among hominoid taxa for the transition between the premaxilla and hard palate to be free of significant topographic relief. However, it is also apparent that this "constraint" on the morphology of the nasal cavity floor can be overridden by the competing spatial demands of the anterior dentition on the morphology of the anterior nasal cavity floor. Comparisons of ontogenetic allometric trajectories suggest that variation in body size, craniofacial orientation and incisor dimensions and inclination may account for some of the interspecific variation observed in hominoid subnasal form. However, a number of questions regarding the developmental basis of the great ape morphology remain unresolved.

With regard to phylogenetic issues, in the absence of additional information either from fossil specimens or comparative developmental anatomy, it is difficult to establish with any certainty the evolutionary polarity of much of the variation observed in hominoid subnasal form. However, it does appear that several features of the orangutan morphology, such as the frequent absence of a prevomer and the reduced diameter of the incisive canal, are derived for this taxon. Although Begun (1992, 1994, 1995) has argued that the *Gorilla* subnasal morphology is primitive for great apes because it shares with *Hylobates* a short premaxilla, "stepped" nasal cavity floor and broad incisive fossa, results of the present study suggest that the

Gorilla morphology is a highly derived morphology that is convergent upon that of hylobatids.

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